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Special Paper Number Two (for 1968): EVOLUTION OF THE SHELL STRUCTURE OF ARTICULATE BRACHIOPODS, by Alwyn Williams. 55 pp., 27 text-figs., 24 collotype plates. Price £5 (U.S. \$13.00).

Special Paper Number Three (for 1968): UPPER MAESTRICHTIAN RADIOLARIA OF CALIFORNIA, by Helen P. Foreman. 83 pp. with 8 collotype plates. Price £3 (U.S. \$8.00).

Typescripts on all aspects of palaeontology and stratigraphical palaeontology are invited. They should conform in style to those already published in this journal, and should be sent to Mr. N. F. Hughes, Department of Geology, Sedgwick Museum, Downing Street, Cambridge, England, who will supply detailed instructions for authors on request (these are published in *Palaeontology*, 10, pp. 707-12).

THE FEEDING MECHANISMS AND AFFINITIES OF THE TRIASSIC BRACHIOPODS *THECOSPIRA* ZUGMAYER AND *BACTRYNIUM* EMMRICH

by M. J. S. RUDWICK

ABSTRACT. The morphology of *Thecospira* and *Bactrynum* is analysed functionally. It is inferred that the spiral brachidium of *Thecospira*, with its unique grooved lamellae, bore a simple spiroloph, and that the 'lobate apparatus' of ridges and grooves in *Bactrynum* bore a complex ptycholoph. The morphology of both genera is consistent with ciliary feeding mechanisms similar to those of living brachiopods: it is inferred that *Thecospira* operated a spirolophous current system of 'exhalant' or 'spirifer' type, analogous to the living *Discinisca*; and that *Bactrynum* operated a ptycholophous system analogous to the living *Megathiris*. Both brachiopods were cemented in early growth stages but later became free-lying; both had a strophic hinge, and normal articulation and musculature. *Bactrynum* is pseudopunctate, *Thecospira* includes punctate and impunctate (or obscurely pseudopunctate) species. Affinity with Permian Davidsoniacea is accepted for *Thecospira*; the nature of its derivation is discussed in functional terms. *Bactrynum* is assigned to the Thecideacea; its resemblance to Permian Lytoniacea is interpreted as due to functional convergence. It is concluded that the Thecideacea were derived from Davidsoniacea, probably during Permian time and probably by neoteny; affinity to Spiriferida or Terebratulida is thus rejected, and the older view reaffirmed, that Thecideacea are surviving Strophomenida. The phylogenetic history of the feeding mechanisms of Thecideacea and *Thecospira* is interpreted in terms of a concept of 'functional zones', and is regarded as an example of 'size-required allometry'.

THE small and rare Triassic brachiopods *Thecospira* and *Bactrynum* are of special interest in the study of the functional evolution of the phylum. Of all the changes in brachiopod faunas between the late Palaeozoic and the early Mesozoic, the most striking is the almost complete disappearance of the Strophomenida. Strophomenides were abundant and diverse in the Permian period, but their representatives in the Triassic are rare, and so changed in form that their affinities have remained controversial.

One such relict strophomenide is the Middle to Upper Triassic *Thecospira*. Its strophomenide affinities are now generally recognized, and it is regarded as the only known post-Palaeozoic davidsoniacean (Williams 1953a, 1965). But it has undergone significant morphological changes, of which the most important is its acquisition of a spiral brachidium with grooved lamellae.

Another relict strophomenide, the late Triassic (Rhaetian) *Bactrynum*, is more problematical. It has a concavo-convex shell resembling that of many Palaeozoic strophomenides. The interior of the dorsal valve bears a series of multi-lobed ridges and grooves which give it a striking resemblance to the Permian lytoniacean *Oldhamina*. On the other hand it was originally regarded as being related to the post-Palaeozoic thecideaceans. The functional analysis of *Bactrynum* in this paper is designed to help to distinguish more clearly those characters that are likely to be due to affinity from those that result from functional parallelism or convergence.

Discussion of *Thecospira* and *Bactrynum* naturally bears on the controversial problem of the affinities of the thecideaceans. Williams's and Rowell's recent contribution to this

problem (1965, pp. H187–9) seems to over-stress features indicating possible affinity to spiriferides or terebratulides, at the expense of those that have previously suggested a connexion with the strophomenides. I believe that a strophomenide affinity for the thecideaceans should be given further consideration.

Taxonomy and material. The genus *Bactrynum* was erected by Emmrich in 1855 for a 'Problematicum' from the Kössener Schichten (Rhaetian) of Austria. *Pterophloios* Gümbel 1861 is a junior synonym. The structure of *Bactrynum* was first clearly described by Zugmayer (1880), who emphasized its similarities to 'Thecidea', i.e., in modern terms, to the Thecideacea. At the same time Zugmayer erected the genus *Thecospira* for small Triassic shells that had previously been assigned to 'Thecidea', but in which he discovered a spiral brachidium of a unique kind.

For some time *Thecospira* was commonly regarded as a spiriferide, purely on account of its brachidium, but Williams (1953a) showed that in all other respects it is clearly related to the Strophomenida, and in the *Treatise* (Williams 1965) it is placed in a monotypic family Thecospiridae within the Davidsoniacea.

The affinities of *Bactrynum* have remained more controversial. Waagen (1883) and Bittner (1890) agreed that it differed from 'Thecidea' and either represented a transition from *Oldhamina* and related genera (i.e. Lyttoniaceae) or else belonged to that group. In their studies of Permian Lyttoniaceae from Timor, Broili (1916) and Wanner (1935) concurred in this judgement; but, on the other hand, Noetling (1905) and Kozłowski (1929) argued that its similarities to the lyttoniaceans were the result of convergence. The former view has been maintained more recently by Stehli (1956); and the latter by Sarycheva (1964), and also by Makridin (1960) in the *Osnovy* (where *Bactrynum* appears under the name *Pterophloios* in the Thecideacea). In the *Treatise*, on the other hand, it is given a monotypic family Bactryniidae, which is placed provisionally among the Lyttoniaceae (Williams 1965).

Bactrynum is known only from the Rhaetian of Austria. Its rarity is such that many features of the morphology remain as obscure as they were in Zugmayer's day. Nevertheless enough can be determined from the available specimens to make a functional reconstruction feasible. I have re-examined Zugmayer's original specimens of the type species *B. bicarinatum* (Emmrich), which are now in the Paläontologisches Institut der Universität, Vienna (PIUW), together with others in the Naturhistorisches Museum, Vienna (NHMW), the U.S. National Museum, Washington (USNM), and the British Museum (Natural History), London (BMNH).

Thecospira is less rare, but is never a common fossil. It has a wider stratigraphical range, from Karnian to Rhaetian, but is confined to the East Alpine region. The best specimens are from the Raibl and St. Cassian beds (Karnian) of the Italian Alps, and from the Kössener and Starhemberger Schichten (Rhaetian) of Austria. I have re-examined Zugmayer's original specimens of the type species *T. haidingeri* (Suess), together with other specimens of that and other species, in the museums already listed. I have also collected *Thecospira* from the St. Cassian beds near Cortina d'Ampezzo; these specimens are now in the Sedgwick Museum, Cambridge (SM).

Acknowledgements. I am particularly grateful to Dr. R. Cowen for invaluable help with the preparation of this paper. I am indebted to Dr. F. Steininger, Professor Dr. H. Zapfe, Dr. G. A. Cooper, and Dr. C. H. C. Brunton, respectively, for access to the collections mentioned above, and for loans of

some specimens. Signor R. Zardini kindly gave advice on field-work, and supplied photographs of specimens in his private collection. My wife gave valuable assistance with collecting, and drew some of the text-figures. Part of this work was done under a research grant from the Science Research Council.

GENERAL FUNCTIONAL MORPHOLOGY

Relation to substratum. Both *Thecospira* and *Bactrynum* are small brachiopods, the largest dimension of the shell being generally less than a centimetre. Both have a roughly elliptical commissure plan, the major axis being transverse in *Thecospira* and longitudinal in *Bactrynum*. In the latter, the commissure may also have a pair of postero-lateral horizontal deflections (cf. Rudwick 1959, p. 10) which produced corresponding ear-like extensions of the valves themselves. The ventral valve of both brachiopods is strongly and fairly uniformly convex. The dorsal valve of *Thecospira* is weakly convex near the umbo, becoming plane and then weakly concave towards the commissure: in other words the convexity was reversed gradually during ontogeny. The dorsal valve of *Bactrynum* is more strongly concave; available specimens do not show clearly whether it too passed through a convex stage early in ontogeny.

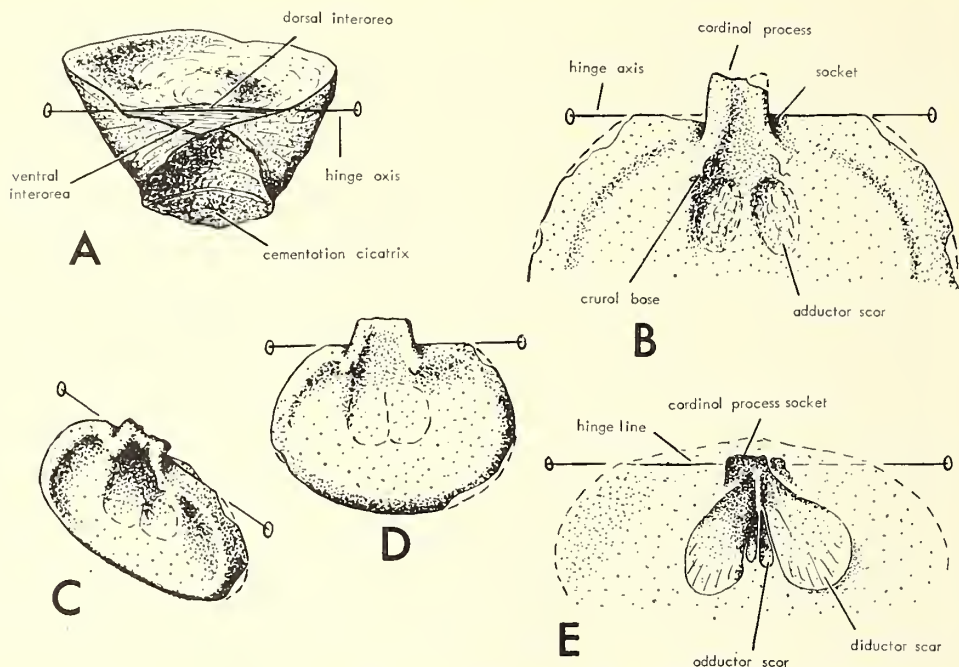
The terms *dorsal valve* and *ventral valve* are used throughout this paper, because *brachial valve* and *pedicle valve* are, in my opinion, misleading and inappropriate: in living articulates neither the brachia nor the pedicle 'belong' to one valve more than the other, in embryonic origin or in adult anatomy; and in many fossil articulates no pedicle existed and there is no direct evidence of the brachia.

There is no trace of a pedicle foramen in either brachiopod, but there is a prominent cicatrix ('scar') of attachment at the apex of the ventral valve. Its appearance suggests that the young shells were generally cemented to shell fragments. The size of the cicatrix shows that when the ventral valve had grown to some 2–4 mm. in breadth its edge began to grow away from the surface of attachment, with consequent increase in the convexity of the valve. Concurrently, at least in *Thecospira*, the dorsal valve became plane and then concave. The orientation of the cicatrix in larger specimens, and its size relative to the whole shell, make it unlikely that the cementation attachment remained effective throughout life. The enclosing argillaceous sediments suggest that apart from scattered shell fragments the substratum was probably soft and muddy. As they grew in size, both brachiopods probably outgrew the shell-fragments on which the spat had settled, and gradually 'heeled over' until they lay freely on the ventral valve, resting on or partly in the soft substratum (text-figs. 8, 10). The ever-increasing convexity of the ventral valve could have ensured that the commissure remained above the surface throughout. A similar relation to the substratum, with an attached stage gradually superseded by a free-lying stage, has probably been common in several brachiopod groups with concavo-convex shells (Rudwick 1965, p. H203; Grant 1966).

Hinge and musculature. There is a moderately broad strophic hinge-line in *Thecospira*. Growth on the hinge-line sectors of the valves produced broad plane interareas on both valves, that on the dorsal valve being very low (text-fig. 1A, Pl. 65, figs. 1, 3; Pl. 66, figs. 17, 18; Pl. 68, figs. 12, 13). Contrary to the description in the *Treatise* (Williams 1965), *Bactrynum* is also strophic, with a very broad hinge-line. This is most clearly seen in a specimen of Zugmayer's, where the dorsal valve is bounded posteriorly by a low plane interarea similar to that of *Thecospira* (text-fig. 2A; Pl. 68, fig. 2). Williams (1965)

notes correctly that the ventral valve shows no trace of the 'posterior flap' of shell material that is characteristic of lyttoniaceans.

In *Thecospira* the pseudodeltidium and chilidium are often precisely flush with the interareas; the growth-lines on the interareas thus cross the mid-line without deflection



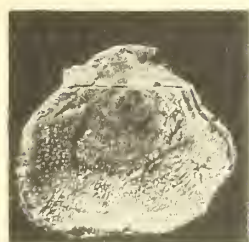
TEXT-FIG. 1. Drawings of *Thecospira*, to illustrate morphology.

- A. Postero-dorsal view of *T. haidingeri* (Suess), $\times 4$ (specimen as in Pl. 65, figs. 1-4).
 B. Ventral view of dorsal valve of *T. tyrolensis* (Loretz), $\times 4$ (specimen as in Pl. 65, figs. 12, 13).
 C. D. Oblique and ventral views of dorsal valve of *T. haidingeri*, $\times 4.5$ (specimen as in Pl. 65, figs. 8, 9).
 E. Dorsal view of ventral valve of *T. haidingeri*, $\times 4.5$ (specimen as in Pl. 65, fig. 7).

(text-fig. 1A; Pl. 65, fig. 1; Pl. 66, figs. 17, 18). In some shells the pseudodeltidium is more clearly delimited (Pl. 68, figs. 11, 12); and there are other Triassic shells originally described as '*Thecidea*', which may in fact be *Thecospira* or closely related to it, in which the pseudodeltidium is slightly but distinctly convex (Pl. 68, fig. 13).

EXPLANATION OF PLATE 65

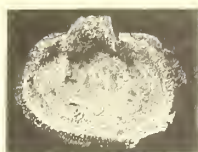
Figs. 1-11. *Thecospira haidingeri* (Suess), Rhaetian, Austria. 1-4, Dorsal, ventral, posterior and left lateral views of whole shell $\times 3$ (PIUW; figured Zugmayer 1880, pl. 2, fig. 33), from Kitzberg. 5-6, Details of ventral and dorsal valve surfaces of same specimen $\times 9$. 7, Interior of ventral valve $\times 3$ (PIUW; figured Zugmayer 1880, pl. 2, fig. 35), from Kitzberg. 8-9, Ventral and oblique posterior views of interior of dorsal valve $\times 3$ (PIUW; figured Zugmayer 1880, pl. 2, fig. 36), from Dürnbach. 10-11, Ventral and oblique posterior views of spiral brachidium in dorsal valve, exposed by grinding and polishing $\times 9$ (PIUW; figured Zugmayer 1880, pl. 2, fig. 39), locality unknown. J, jugum; C, crus. 12-13, *Thecospira tyrolensis* (Loretz), Raibler Schichten, Romerlo, near Cortina d'Ampezzo, Italy. Ventral and oblique posterior views of interior of dorsal valve $\times 3$ (NHMW).



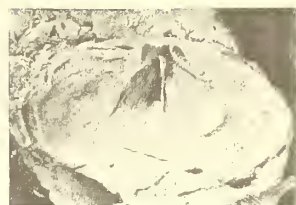
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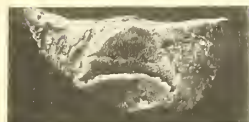
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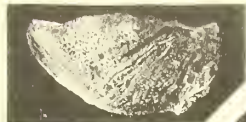
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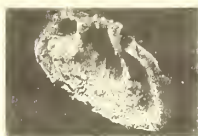
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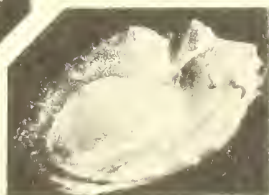
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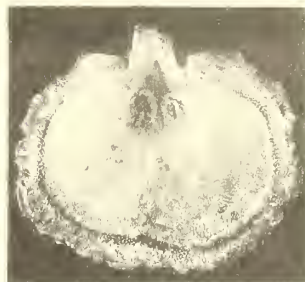
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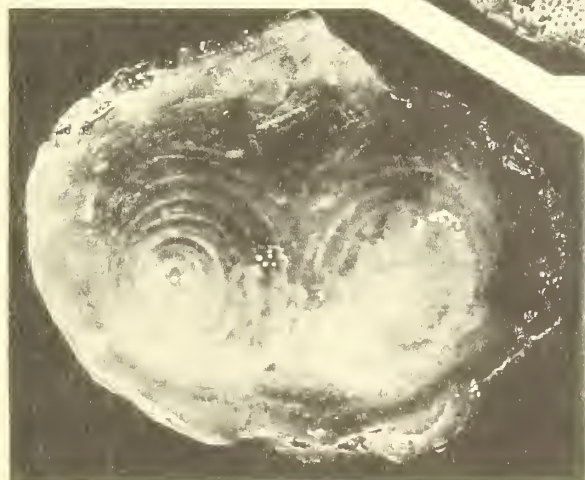
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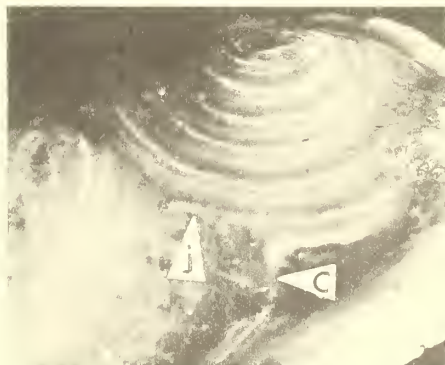
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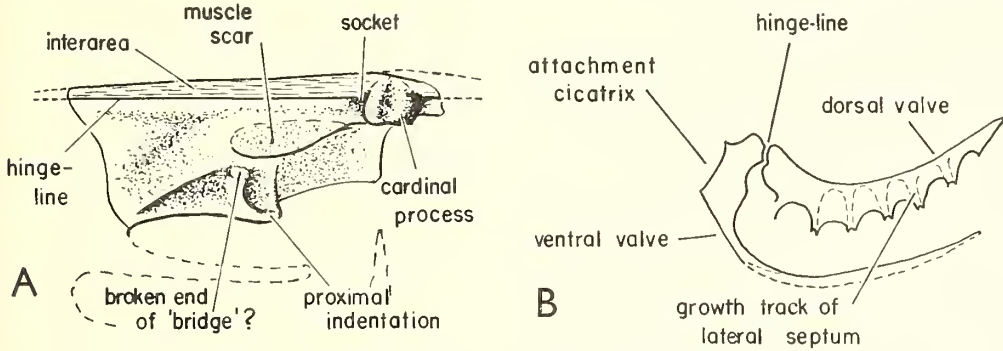
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The form of the pseudodeltidium and chilidium in *Bactrynum* are not known with certainty. The fragmentary dorsal valve already referred to is not well enough preserved to show the chilidium clearly, though it was probably convex and arched over the base of the cardinal process. '*Thecidea bicarinata*' Klipstein, which may be congeneric, has a convex pseudodeltidium and chilidium.

Thecospira has a pair of strong teeth, unsupported by dental lamellae, projecting forwards from beneath the pseudodeltidium (Pl. 68, fig. 11). The corresponding sockets are defined medially by the sides of the large rectangular cardinal process, and anteriorly by 'socket plates', which are simply low ridges formed by the sides of the cardinal



TEXT-FIG. 2. Morphology of *Bactrynum*.

- A. Postero-ventral view of fragment of dorsal valve, showing strophic hinge and low interarea, cardinalia, muscle scar, and posterior region of 'lobate apparatus', $\times 10$ (specimen as in Pl. 68, fig. 1, 2).
 B. Longitudinal section through shell, showing concavo-convex form, with growth tracks of lateral septa, $\times 5$ (specimen as in Pl. 68, fig. 9).

process curving antero-laterally to merge with the floor of the valve (text-fig. 1B-D; Pl. 65, figs. 8, 9, 12, 13; Pl. 66, fig. 16). The teeth of *Bactrynum* are not yet known, but the cardinalia in the dorsal valve are very similar to those of *Thecospira*, though the cardinal process is relatively smaller (text-fig. 2A; Pl. 68, fig. 1, 2). These hinge structures are in no way abnormal.

The degree of rotation possible with this articulation cannot easily be inferred. The hinges have some mechanical resemblance to that of the living *Lacazella*, in which the angle of opening approaches 90° (Lacaze-Duthiers 1861). Possibly the shells of *Thecospira* and *Bactrynum* opened to a similar extent. The feeding mechanisms reconstructed in this paper would be feasible with either a small or large angle of opening.

The cardinal process of *Thecospira* is indistinctly bilobed (text-fig. 1B-D; Pl. 65, figs. 8, 9, 12, 13; Pl. 68, fig. 12), and the diductor attachments are visible distally. The cardinal process projects into a deep cavity beneath the pseudodeltidium (Pl. 68, figs. 11, 12). On the floor of the ventral valve the diductor attachments are large and flabellate (text-fig. 1E; Pl. 65, fig. 7). Between them are the narrow lanceolate attachments of the adductors. I have not seen the median septum in the ventral valve mentioned in the *Treatise* description. The adductor scars on the dorsal valve are elliptical, are not divided into anterior and posterior pairs, and are separated in the mid-line by a long narrow ridge (text-fig. 1B-D; Pl. 65, figs. 8, 13; Pl. 66, fig. 16).

The cardinal process of *Bactrynum* is also indistinctly bilobed. Lateral to its base is a smooth transversely elliptical area (text-fig. 2A; Pl. 68, fig. 2), which closely resembles the scar of the 'lateral adductor' muscle in the living *Lacazella* and the similar scars in Jurassic thecideaceans such as *Eudesella* and *Davidsonella* (Pl. 68, figs. 3, 4). No other scars are visible on the dorsal valve, but the preservation is not ideal; the scars on the ventral valve are not known at all.

In *Thecospira* the muscular leverage involved in opening and closing the shell was in no way unusual. The musculature is here reconstructed (text-fig. 8) on the conjectural assumption that the muscles were columnar (as in living thecideaceans and inarticulates) and not tendonous (as in living rhynchonellides and terebratulides). If the adductors were differentiated into striated 'quick' and unstriated 'catch' portions, these portions were not separated spatially like the anterior and posterior adductors of living rhynchonellides and terebratulides. The orientation of the diductors shows that a wide degree of opening of the shell would have been mechanically possible, if allowed by the articulation.

As far as available evidence goes, the muscular leverage of *Bactrynum* was also 'normal', apart from the lateral shift of the main adductors, which is also known in the thecideaceans.

In both brachiopods the soft tissues would have been sealed extremely effectively and strongly when the shell was closed, for the lid-like dorsal valve has a strongly thickened submarginal rim (text-fig. 1B-D; Pl. 65, figs. 8, 9, 12, 13).

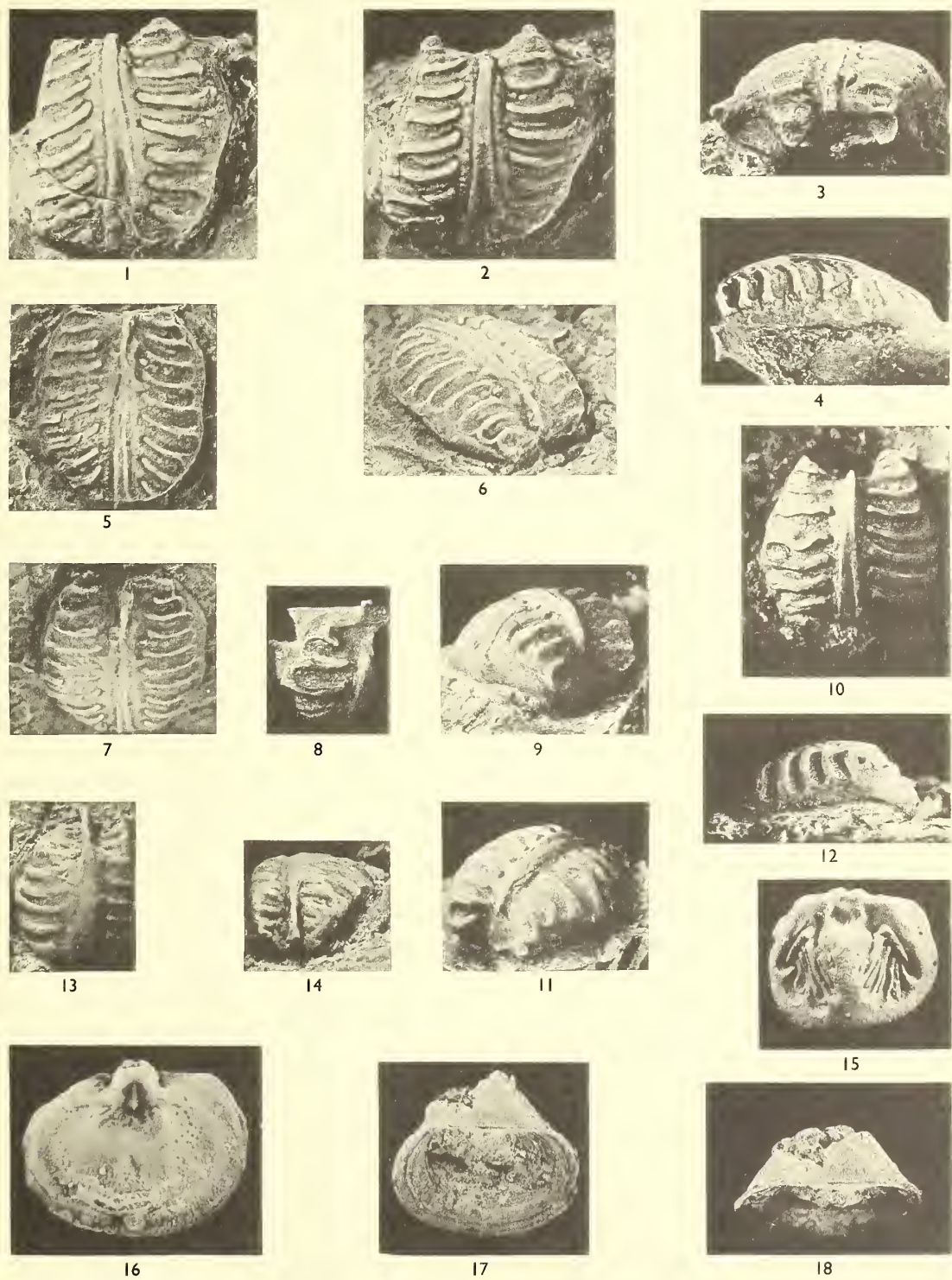
'Ornament' and shell structure. Primary-layer shell covers the exterior of both valves in the normal way. In *Bactrynum* it is marked only with finely wrinkled growth-lines (cf. Bittner 1890, pl. 26, fig. 18). In *Thecospira* there are small tear-shaped pustules, oriented radially and apparently scattered over the entire shell surface (Pl. 65, figs. 5, 6). Where best preserved, they appear to have been short slender spinelets (Pl. 65, fig. 6, central area of dorsal valve); and among them are faint traces of radial costellae (Pl. 65, fig. 6, umbonal region). Some shells from the Cortina area have fewer pustules and much more conspicuous radial costellae, with new costellae added by intercalation (Pl. 68, fig. 12). There are no large tubular spines of productoid type on either brachiopod.

A detailed study of shell structure is beyond the scope of this paper, but the known structures must be mentioned briefly in view of their prominence in discussions on affinity. *Bactrynum* is said to be pseudopunctate (Williams 1965), and this seems to be

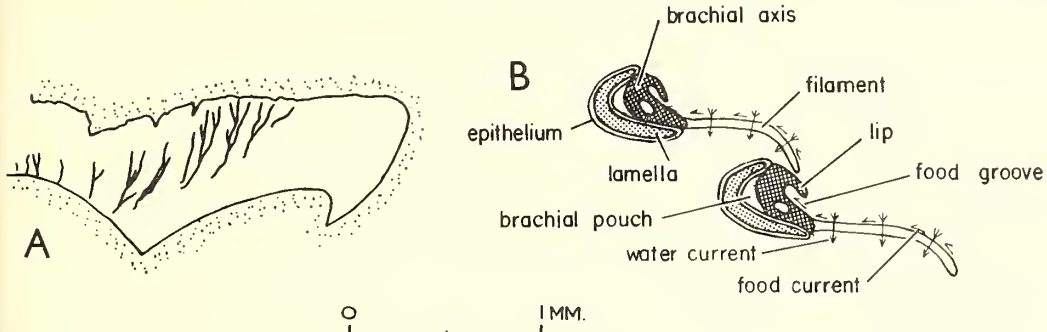
EXPLANATION OF PLATE 66

All figures $\times 3$. Figs. 1-7, 13-18 are whitened with ammonium chloride.

Figs. 1-14. *Bactrynum bicarinatum* Emmrich, from the Kössener Schichten, Austria. 1-4, Ventral, postero-ventral, posterior and left lateral views of interior of dorsal valve of USNM 108873, from Baytal, Gumpoldskirchen, near Vienna (Williams 1965, fig. 397 shows same specimen before posterior spike was broken off). 5-7, Ventral, oblique and postero-ventral views of interior of dorsal valve of USNM 129877a, from the same locality. 8, Interior of fragment of dorsal valve from Dürnbach (PIUW; figured Zugmayer 1880, pl. 2, fig. 18). 9-12, Right oblique, ventral, left oblique and right lateral views of interior of dorsal valve of specimen from the same locality (NHMW). 13, 14, Ventral and posterior views of interior of dorsal valve of USNM 129877b, from Baytal. 15, *Thecidiopsis hieroglyphica* (Goldfuss), from the Maestrichtian (late Cretaceous) of Limburg, Holland. Interior of dorsal valve of SM.F.3111. 16-18, *Thecospira* sp., from the St. Cassianer Schichten, Alpe di Specie (Seelandalpe), near Cortina d'Ampezzo, Italy. 16, Interior of dorsal valve of SM.G.1261. 17, 18, Postero-dorsal and posterior views of SM.G.1262.



confirmed by a study of Zugmayer's original sections, though these are crude by modern standards. The structure of *Thecospira* is more problematical. Suess noted in his original description of *T. haidingeri* that it was punctate (1854, p. 44), and this is very clearly shown by Zugmayer's specimens (Pl. 65, figs. 5, 6). But Bittner (1890) commented that although some species are punctate, others are apparently impunctate. Cellulose peels taken from several specimens confirm that there is a genuine diversity of shell structure within the genus. This must clearly be taken into account in any future systematic revision; for the present, it is sufficient to outline the nature of the diversity.



TEXT-FIG. 3. Morphology of *Thecospira*.

- A. Diagram based on a polished longitudinal section through a dorsal valve of *Thecospira* sp., showing punctae coalescing as they traverse the shell; external surface above. More punctae are shown than actually lie in the plane of the section; since they are picked out by matrix they are visible for a further part of their course. St. Cassianer Schichten, Alpe di Specie, near Cortina d'Ampezzo, Italy; SM.G.1260.
- B. Reconstruction of brachium of *Thecospira*: cross-sections of two adjacent whorls, with filaments in inferred natural orientation; for further explanation see text.

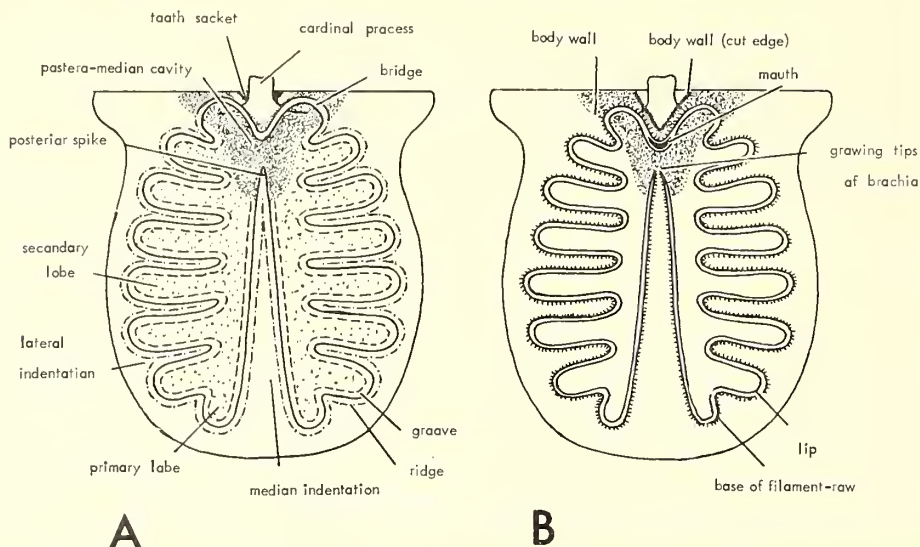
Specimens of *Thecospira* sp., from the St. Cassian beds of the Alpe di Specie [Seelandalpe], near Cortina, are punctate, but the punctation is most unusual. Closely spaced, thick punctae of the exterior shell layers coalesce into comparatively few, more widely spaced punctae as they cross the shell thickness (text-fig. 3A). Probably the structure is the same as that described loosely by Bittner in *Thecospira davidsoni* (1890, p. 287). Similar types of punctation are known elsewhere in the phylum only in some inarticulate brachiopods (e.g. *Crania*) and in the Silurian enteletacean *Dicoelosia* (Wright 1966); but all three occurrences of this type of punctation are likely to represent independent developments of the structure.

T. tyrolensis (Loretz) is impunctate, but the shell structure appears complex because of the presence of small pimples or pustules on the inner surface of the valves. As shell growth proceeds, the pustules are incorporated in the secondary shell layer. *T. guembeli* (Pichler), on the other hand, has a shell structure which can be regarded as obscurely pseudopunctate; there is a 'normal' primary and secondary-layer structure with an inner layer in which the orientation of the crystals is irregular.

Coelom and body wall. In living articulates the coelom, bounded by the body wall and containing the muscles, gut, etc., is confined to a small postero-median part of the shell cavity. The body-wall is 'wrapped' closely round the anterior and lateral surfaces of the

muscles, and laterally it incorporates the crura. A consistent reconstruction of the body wall of *Thecospira* can be made by homology. The crura or 'apophyses' project forwards from the 'socket plates' at the base of the cardinal process, in a position consistent with a body-wall wrapped around the lateral surfaces of the muscles (text-figs. 1B-D, 8, 9).

A reconstruction of the gut, though given here for the sake of completeness, is necessarily conjectural. Its position and form as shown (text-fig. 9) are, however, consistent with what is known of living articulates. An enlarged stomach and lateral digestive glands would have fitted neatly into the space (otherwise empty) behind the adductors



TEXT-FIG. 4. Diagrams to show (A) morphology of 'lobate apparatus' on dorsal valve of *Bactrynum*, and (B) its interpretation as a supporting structure for a complex ptycholophous lophophore.

and above the diductors, occupying also the concavity at the base of the cardinal process (text-fig. 1B-D; Pl. 65, figs. 9, 13; Pl. 66, fig. 16).

When the shell of *Bactrynum* is preserved closed there is little space between the ridged internal surface of the dorsal valve and the corresponding surface of the ventral valve. Posteriorly, however, the dorsal valve is 'excavated' (strictly speaking, it is not thickened like the rest of the valve) into a broad median cavity (text-fig. 4A; Pl. 66, figs. 2, 10). There is a similar cavity in thecideaceans (Pl. 66, fig. 15), and in the living *Lacazella* this is known to accommodate the dorsal part of the 'body' (coelom) with viscera and muscles. It is, therefore, reasonable to infer that the 'body' of *Bactrynum*, like that of *Thecospira*, was confined to a small median-posterior portion of the shell cavity (text-fig. 4B).

THE LOPHOPHORE

The brachidium in Thecospira. The spiral brachidium of *Thecospira* consists of a pair of low conical spiralia, attached to the dorsal valve by a pair of crura or 'apophyses', and linked to each other proximally, across the median plane, by a simple jugum.

The crura are short peg-like processes, circular in cross-section, which project forwards from the 'socket plates' near the base of the cardinal process. In most specimens they are broken off, and their position is only shown by a pair of small residual tubercles on the 'socket plates' (text-fig. 1B-D; Pl. 65, figs. 9, 12). Their connexion with the spiralia is, however, visible on Zugmayer's ground and polished specimen (Pl. 65, fig. 11). The crura manifestly had the same function as the crura of other brachiopods, and they project from the cardinalia in essentially the same way; therefore it seems hardly necessary to distinguish them by another term ('apophyses', cf. Williams 1965). The differences, which are part of the evidence for regarding the brachidium of *Thecospira* as a separate development, are in the cardinalia rather than the crura themselves.

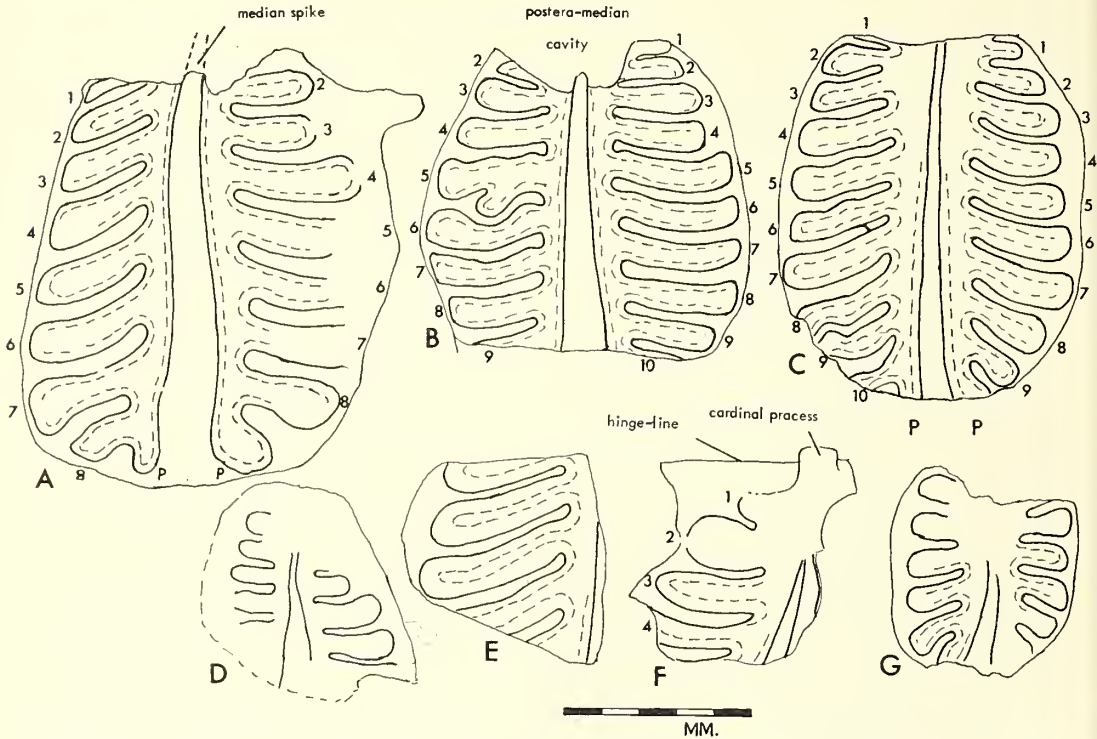
The spiral axis of each spiraliun is inclined, with the apex of the spiral pointing latero-ventrally. The spiralia occupy almost the whole of the shell cavity, and when the shell is closed the spiral lamellae lie very close to the internal surface of the ventral valve (cf. Bittner 1890, text-fig., p. 310). The lamella is unique, as Zugmayer emphasized, by being U-shaped in cross-section. No such gutter-like lamella is known in any of the Spiriferida. The gutter faces outwards around the spiral (Pl. 65, figs. 10, 11). The ventral limb of the 'U' is narrower than the dorsal. The ventral side passes proximally into the jugum, the dorsal into the crura. The structure of the jugum is not very clear in Zugmayer's specimens, and it has not been detected with certainty in serial cellulose peels. Possibly it consists only of crural processes, projecting towards the mid-line without meeting each other (Pl. 65, fig. 11).

Lobate apparatus of Bactrynum. On the internal surface of the dorsal valve of *Bactrynum* there is a series of lobed ridges and grooves. This 'lobate apparatus' is approximately, but not accurately, symmetrical about the median plane. It consists of a pair of longitudinally elongated *primary lobes* separated by a long *median indentation*, and up to ten pairs of laterally elongated *secondary lobes* projecting laterally from the primary lobes and separated from one another by *lateral indentations* (text-fig. 4A). An occasional *tertiary lobe* branches from a secondary lobe as a minor irregularity (text-fig. 5B, lobe 5 left). The lobes have sub-parallel sides, and approximate to a uniform width of about 0.9 mm. in all parts of all specimens (text-fig. 5). The lateral indentations likewise have sub-parallel sides, and approximate to a uniform width of about 0.3 mm. The median indentation has a similar width posteriorly, but broadens anteriorly. (The uniform width of the lobes and indentations is partly obscured in text-fig. 5 by the foreshortening of the peripheral parts, due to the strong convexity of the internal surface of the valve.)

The lobes and indentations are outlined by the sinuous course of a closely contiguous groove and ridge (text-fig. 4A). These can be seen with variable clarity in different specimens; this is partly due to differences of preservation, but there may be some genuine variation. The groove is internal in position, the ridge external. The steep slope between them is always clearest: the course of this outer edge of the groove (or inner edge of the ridge) is shown by a continuous line in text-figs. 4A and 5, and is the basis of the measurements given above.

The ridge is clearly visible, and clearly raised above the rest of the valve surface, in the broad anterior part of the median indentation (Pl. 66, figs. 1, 2, 5-7, 10). In the narrower posterior part the ridges of the left and right sides generally coalesce into

a single ridge; but in the best-preserved specimens the median indentation is clearly 'double' right to its tip (Pl. 67, fig. 5; Pl. 68, fig. 1). The posterior tip of the median indentation projects as a conspicuous *spike* overhanging the postero-median cavity (Pl. 66, figs. 1, 10): this spike is vulnerable to damage and has generally been broken off at its base. As in the median indentation, the ridges on either side of each lateral

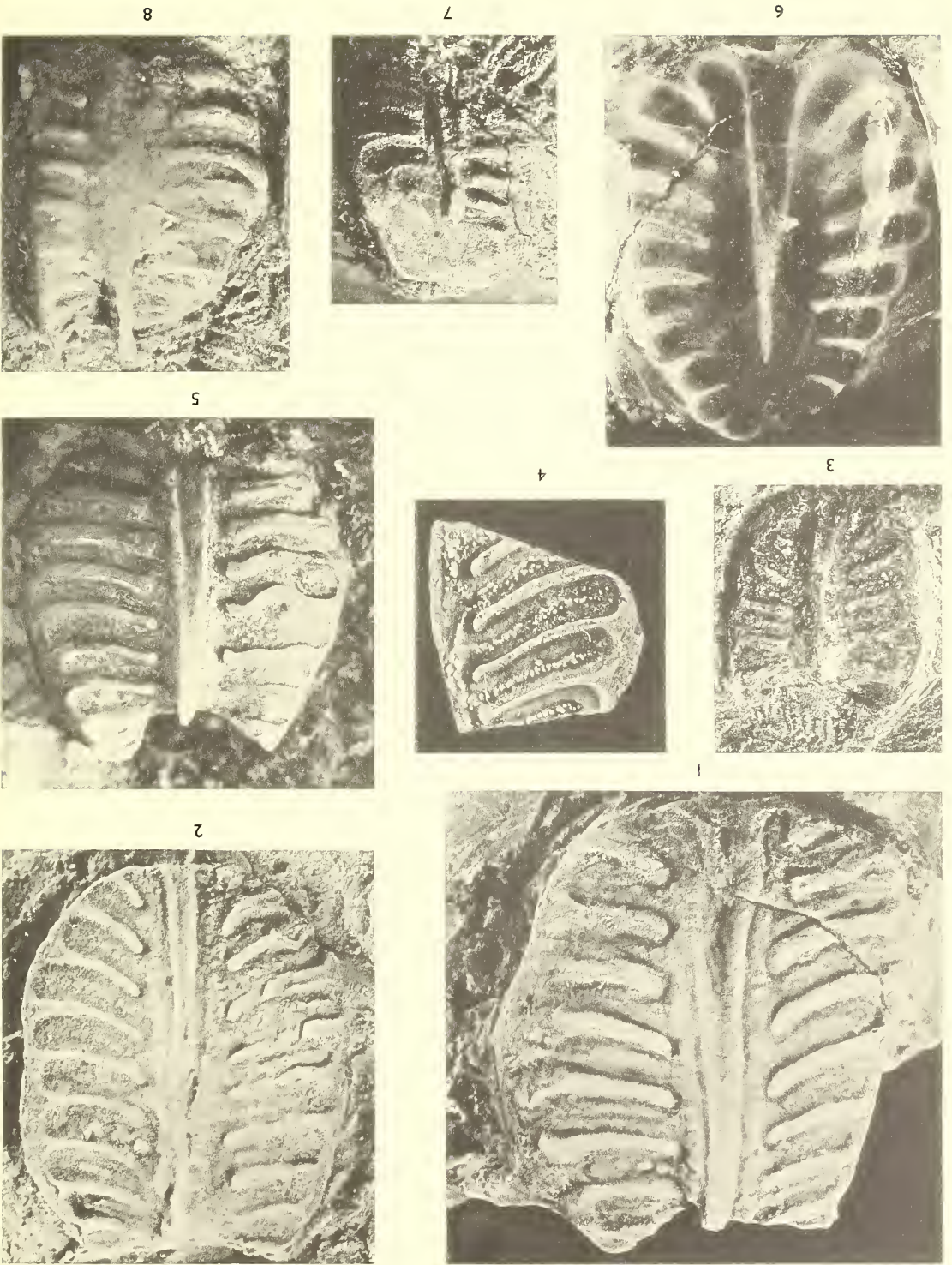


TEXT-FIG. 5. Drawings of the 'lobate apparatus' on dorsal valves of *Bactrynum*, to show uniformity of dimensions of lobes and indentations, all $\times 5$. Continuous line indicates slope between groove and ridge; dashed line, inner edge of groove. (Details of specimens given in captions to plates: A, as Pl. 66, figs. 1, 2; B, as Pl. 66, figs. 9-12; C, as Pl. 66, figs. 5-7; D, as Pl. 67, fig. 7; E, as Pl. 67, fig. 4; F, as Pl. 66, fig. 8; G, as Pl. 67, fig. 3.) Scale represents 5 mm.

EXPLANATION OF PLATE 67

Figs. 1-8. *Bactrynum bicarinatum* Emmerich, from the Kössener Schichten of Austria. All figures $\times 6$; figs. 1-4, 7-8 are whitened with ammonium chloride.

1, 2, Internal surface of dorsal valves, enlarged from Pl. 66, figs. 1 and 5 respectively, to show lobed groove and pustular area within groove. 3, Internal surface of dorsal valve of small (young?) specimen from Kössen, to show smaller number but similar dimensions of lobes (PIUW; figured Zugmayer 1880, pl. 2, fig. 17). 4, Internal surface of fragment of dorsal valve from Kitzberg, to show pustular area within groove (PIUW; figured Zugmayer 1880, pl. 2, fig. 20). 5, Internal surface of dorsal valve, enlarged from Pl. 66, fig. 10, to show postero-median cavity and minor irregularities in lateral lobes. 6, Dorsal valve ground down to show lateral indentations, median spike, and posterior bridge (PIUW; Zugmayer coll.; specimen coated with oil before photographing). 7, Internal surface of dorsal valve of small (young?) specimen from Kössen; compare with fig. 3 (BMNH B.2103). 8, Internal surface of dorsal valve, enlarged from Pl. 66, fig. 13.



indentation are often coalesced into a single ridge or 'lateral septum'; but here too the best specimens show that the ridge is double in origin (Pl. 67, fig. 4; Pl. 68, fig. 1). Around the distal end of each lobe the ridge may be clearly marked or may merge insensibly into the peripheral part of the valve surface.

The groove likewise is variably expressed; it may be clearly differentiated from the central area of the lobes or may merge insensibly into it. Where the inner edge of the groove is distinct, it is shown by a dashed line in text-fig. 5. The central area of the lobes is differentiated, at least in the best specimens, by a distinctly pustular surface (Pl. 67, figs. 2-5).

The posterior extremity of the groove/ridge structure is not entirely clear. The most posterior pair of secondary lobes are generally short, and lie antero-lateral to the cardinal process. At first sight it might appear that the groove runs into the base of the cardinal process (Pl. 66, figs. 3, 8, 11; cf. Williams 1965, p. H521). But this is an illusion. A specimen of Zugmayer's, ground down to expose the ridges, shows clearly that the ridges of left and right sides fused with one another in the median plane to form a forwardly projecting V-shaped structure (Pl. 67, fig. 6). Zugmayer himself referred to this as a *bridge*, and this interpretation appears to me to be correct. In other words, at points antero-lateral to the cardinal process the ridge rises away from the floor of the valve and crosses the postero-median cavity as a bridge-like lamella (text-fig. 4A). In the best-preserved specimens (Pl. 66, fig. 3; Pl. 68, fig. 1) the ridges appear to end abruptly, but these are evidently breakage surfaces at the points where the ridges became a free lamella. It is clearly distinct from the 'socket plate' running into the base of the cardinal process (text-fig. 2A).

Brachial axis of Thecospira. The entire brachidium of *Thecospira*, like that of any other articulate, is clearly an outgrowth of the secondary-layer material of the dorsal valve. As such, it must have been sheathed by, and secreted by, an extension of the outer mantle epithelium (cf. Williams 1956). As with the spiral brachidia of spiriferides, geometrical considerations alone are sufficient to prove that this epithelium must have had the power of resorption as well as secretion, or else the brachidium could not have grown in size while retaining its form and relative position.

In their reconstruction of the lophophore of spiriferides, Williams and Wright (1961) make the assumption that the growing tips of the brachia necessarily remained together in the mid-line, on the jugum, throughout ontogeny. But this assumption is not fully supported even by their cited analogy of plectolophes in living brachiopods; in *Gryphus vitreus*, for example, the growing tips are far apart from one another at the distal end of the median coil. Even supposing that a complete jugum was present in *Thecospira*, therefore, I see no justification for reconstructing a 'deuterolophe' (i.e. doubled brachial axes) on the spiral lamellae. The simpler reconstruction of an ordinary spirolophe seems to me more plausible, in view of the close resemblance between the form of the spiral brachidium and that of the spiral lophophores of living rhynchonellides.

On this reconstruction each whorl of the lamellae would have borne a corresponding single whorl of the brachial axis, and the growing tips of the brachia were at the tips of the lamellae. As suggested previously (Rudwick 1960, text-fig. 6D), the brachial axis is shown, conjecturally, nestling within the 'gutter'; if this is correct the filament-row, at least near its base, would have projected outwards around each whorl. If the lophophore

was supported throughout its length by the brachidium, the great brachial canal, which in most living articulate acts as a hydrostatic skeleton, may have been vestigial or absent; and it is so shown, conjecturally, in the reconstruction given here (text-fig. 3B).

Proximally, by homology with living brachiopods, the axis would have continued towards the mid-line, lying adjacent to the crural processes or jugum. The mouth would have been situated in the mid-line. At this point, if the basic orientation of the lophophore was like that of all living brachiopods, the filament-row must have been on the posterior or ventral side of the mouth and food-groove, and the lip on the anterior or dorsal side. Then, by tracing the axis laterally on to the spirals, it follows by simple topology that the filament-row must have been on the *dorsal* side of the food-groove, and the lip on the ventral, on each of the outwardly facing whorls of the spirolophes. The brachial axis is similarly twisted in the proximal parts of the spirolophes and plectolophes of living brachiopods (Rudwick 1962, text-figs. 7c, 9c, 12b).

Brachial axis of Bactrynum. The mode of growth of the lobate apparatus can be inferred quite simply (text-fig. 6). A section of Zugmayer's, cut longitudinally through the dorsal valve parallel to the median plane, shows clearly that the lobate apparatus grew by simple accretion. The 'lateral septa' (i.e. the coalesced doubled ridges in the lateral indentations) remained in the same absolute position during the growth of the valve, for their growth tracks can be seen projecting through the thickness of the valve perpendicular to its outer surface (text-fig. 2B; Pl. 68, fig. 9). Since the valve grew not only in thickness but also in area, any given lobe must therefore have changed in *relative* position during ontogeny, becoming progressively more posterior. The distal ends of the lobes are near the valve edge in specimens of all sizes: therefore the lobes must have grown in

EXPLANATION OF PLATE 68

Bactrynum, *Thecospira* and other brachiopods for comparison. All figures $\times 6$. All except fig. 9 whitened with ammonium chloride.

Figs. 1, 2. *Bactrynum bicarinatum* Emmerich; ventral and posterior views of fragment of dorsal valve; see also text-fig. 2A. Kössener Schichten of Dürnbach (PIUW; figured Zugmayer 1880, pl. 2, fig. 18).

Fig. 3. *Eudesella mayalis* (Deslongchamps), from the 'Couche à Leptaena' (Upper Lias), of May, Calvados, France; interior of dorsal valve (SM.F.20273).

Figs. 4, 5. *Davidsonella sinuata* (Deslongchamps), from the same locality and horizon; postero-ventral and ventral views of dorsal valve (SM.F.20199).

Fig. 6. *Moorellia leptaenoides* (Deslongchamps), from the same locality and horizon; interior of dorsal valve (SM.F.20258).

Figs. 7, 8. *Elliottia deslongchampsii* (Davidson), from the Middle Lias of May, Calvados, France; ventral and postero-ventral views of dorsal valve (SM.F.20288).

Fig. 9. *Bactrynum bicarinatum* Emmerich, longitudinal section of dorsal valve (and part of ventral), showing growth tracks of lateral septa; see also text-fig. 2B. (PIUW; figured Zugmayer 1880, pl. 2, fig. 32.) Locality unknown.

Fig. 10. *Lyttonia* sp., internal surface of part of dorsal valve, for comparison with *Bactrynum*. Sandy limestone beds above Middle Productus Limestone (Permian), Banshang, East of Chideru, Salt Range, Pakistan (Yale University, Peabody Museum, 22954).

Figs. 11, 12. *Thecospira* sp. Dorsal views of ventral valve alone and of both valves as found in loose association, to show pseudodeltidium, articulation and radial costellae. Raibler Schichten, Rumerlo, near Cortina d'Ampezzo, Italy (R. Zardini coll.).

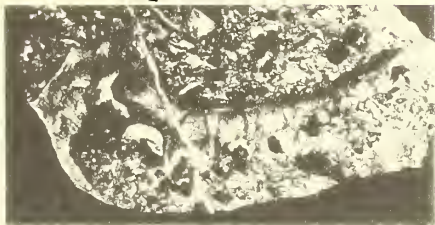
Fig. 13. '*Thecidea* sp.' (*Thecospira*?), dorsal view of shell, to show convex pseudodeltidium, from Helenenthal, Baden (PIUW; figured Zugmayer 1880, pl. 2, fig. 41).



1



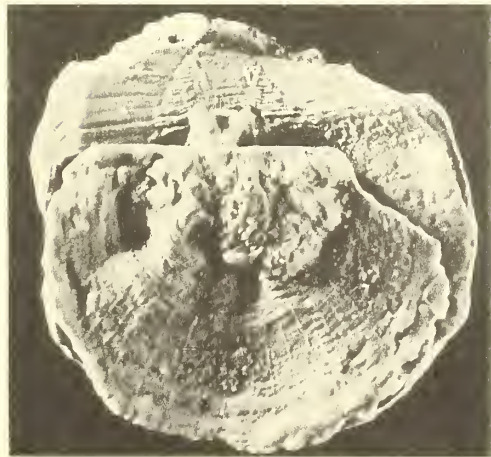
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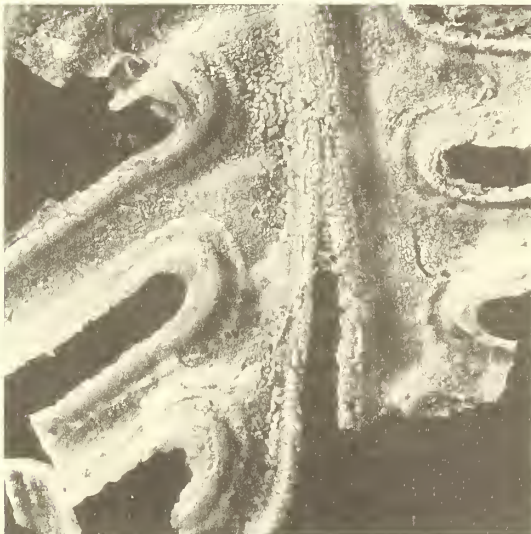
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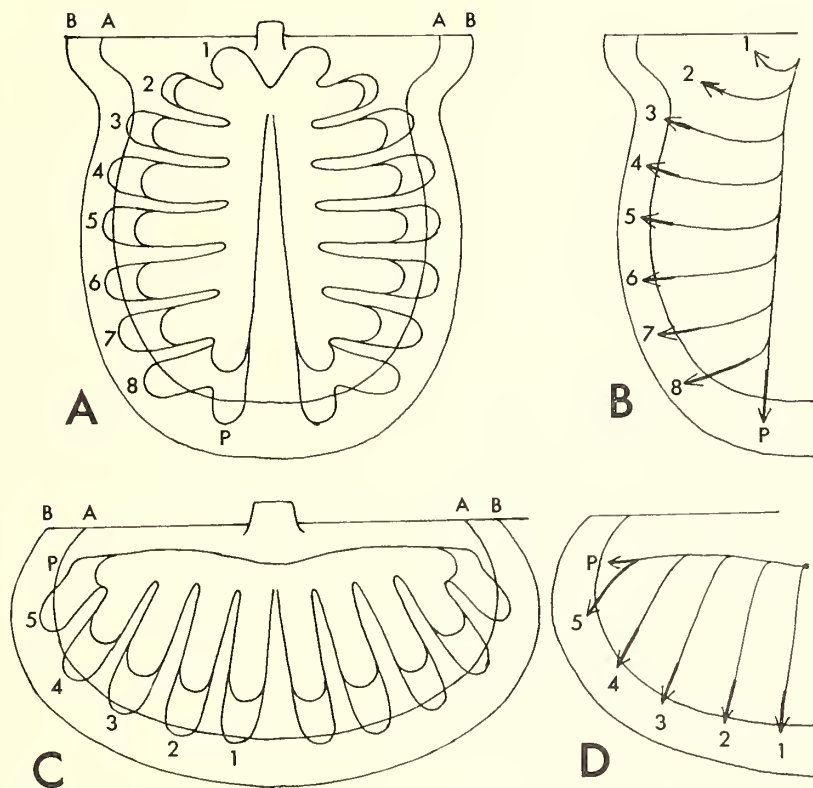


10



13

length during ontogeny, extending laterally as the valve increased in breadth. At the same time the valve was also growing in length, and therefore the most anterior secondary lobe must have become progressively further from the anterior edge of the valve. But the most anterior secondary lobes, and the primary lobes themselves, are near the anterior edge in specimens of all sizes: therefore new secondary lobes must have been



TEXT-FIG. 6. Diagrams to show inferred mode of growth of 'lobate apparatus' of *Bactrynum* (A, B), compared with *Thecidiopsis* (C, D). Figs. A, C show course of lobed groove and ridge; figs. B, D show corresponding growth tracks of axes of lobes; lobes are numbered consecutively in order of derivation from the persistent primary lobes P. As dorsal valve grows in size from AA to BB, lobes grow in length but do not change in absolute position; new lobes (no. 8 in fig. A, no. 5 in fig. C) are budded off from persistent primary lobes.

budded off at intervals during ontogeny from the pair of persistent primary lobes. Thus in text-fig. 6A, during growth of the valve margin from AA to BB, secondary lobes 1 to 7 extended laterally while remaining in the same absolute position on the valve, while the primary lobe extended forwards and budded off the new secondary lobe 8. The whole process of growth of the lobate apparatus could have been achieved simply by differential rates of secretion of shell material over the surface of the valve as it increased in thickness and over-all size: there is no need to postulate any shell resorption (except possibly on the posterior edge of the 'bridge').

This analysis of growth justifies the terminology so far used in a purely descriptive sense. The primary lobe may be so called because it must have persisted throughout ontogeny in a submedian position, growing progressively forwards. The secondary lobes must all have been derived from the primary lobe by lateral budding, in order from the most posterior lobe forwards. The numbering of the secondary lobes thus corresponds to their order of appearance (text-fig. 6B).

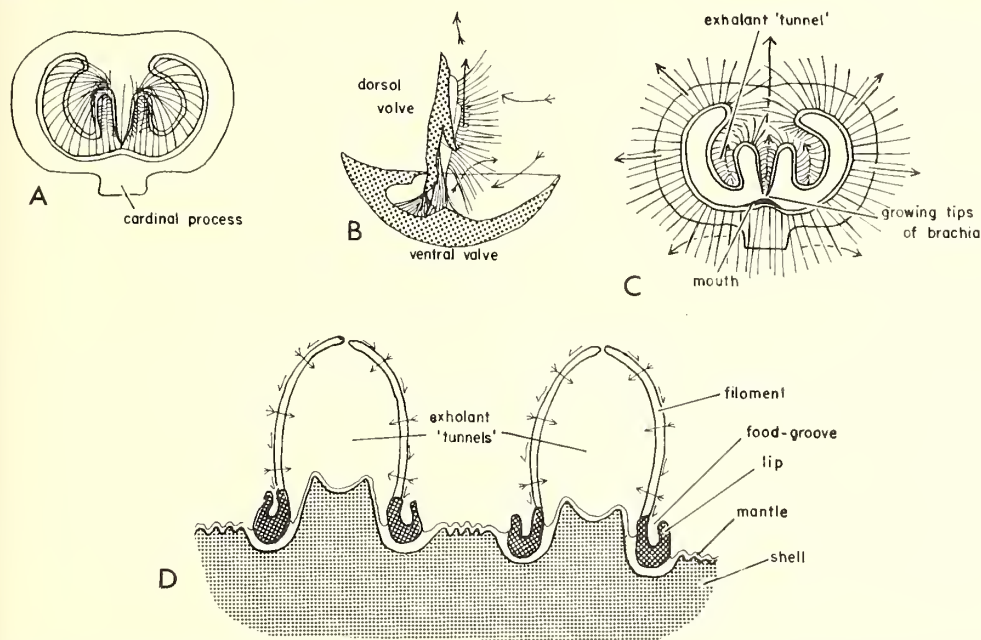
The over-all effect of the growth of the lobate apparatus was to keep the internal surface of the valve fully covered (except in the peripheral zone) with a series of lobes and indentations of a constant standard width, whatever the absolute size and area of the valve.

There is a close analogy between the lobate apparatus of *Bactrynum* and the brachia-bearing grooves and ridges in living Thecideacea. On the inner surface of the dorsal valve there is a lobed groove, two-lobed in *Thecidellina*, four-lobed in *Lacazella* (Elliott 1965, fig. 742, 3a; 744, 2a). On the outer side the groove is separated by a conspicuous slope from an outer ridge, though the latter may not be clearly distinguishable from the peripheral zone of the valve. Postero-laterally the outer ridge extends freely above the postero-median cavity, projecting towards the mid-line, or it may fuse with that projecting from the opposite side to form a complete bridge over the cavity. This bridge is clearly separate from the 'socket plates' and cardinal process. In the median indentation the ridges of left and right sides gradually coalesce and project backwards as a spike overhanging the postero-median cavity. Indeed in *Lacazella* all the 'septa' in the indentations may overhang in this way at their inner ends. Internal to the lobed groove is a second, inner ridge, the so-called 'brachial ridge'; within each lobe this is clearly double in origin, but may be coalesced into a single ridge running along the axis of the lobe. This inner ridge, like the outer, may project freely so as to overhang the postero-median cavity. Its crest is often distinctly pustular.

Although the anatomy of living thecideaceans remains imperfectly known in many respects, it is at least clear that the brachial axis of the lophophore is attached throughout its length to the dorsal mantle, and that it lies in the lobed groove. This can be seen in both *Thecidellina* (cf. Elliott 1965, fig. 742, 3a) and in *Lacazella* (Lacaze-Duthiers 1861, pl. 3, fig. 1). The frontal side of the axis, bearing the lip, faces inwards, towards the inner 'brachial' ridge; while the outer side, bearing the filament-row, faces outwards, towards the outer ridge. The distal growing tips of the brachial axis are located close together at the tip of the median indentation (Lacaze-Duthiers 1861, pl. 2, fig. 7). The mouth is located medially, on the anterior side of the bridge over the postero-median cavity. The arrangement of the lobes is such that the lophophore of *Thecidellina* is a schizolophe, while that of *Lacazella* is a simple (four-lobed) ptycholophe. (Williams's and Rowell's (1965, p. H38) novel definition of the trocholophous stage, to include all lophophores in which the filaments are arranged in a single series, seems to me to be unwarranted: lophophore growth stages were originally defined by the arrangement of the brachial axis, and should remain so.)

The brachial axis of *Bactrynum* may be reconstructed in a comparable position, attached to the dorsal mantle and lying in the lobed groove, with the filament-row facing the outer bounding ridge and the lip facing the inner pustular area (text-fig. 7D). Then proximally, at the mouth, the axis would have had the normal orientation, with the filament-row on the posterior or ventral side of the mouth and the lip on the anterior

or dorsal side. Thus the lophophore would have been a complex ptycholophe, with up to twenty or more lobes (text-fig. 4B). It may be assumed that the lophophore would have grown, like those of all living brachiopods, only by the lengthening of the brachial axis and the formation of new filaments at the extreme tip of the brachia, in the median indentation. Any given filament would therefore have shifted continually in its *relative* position during the growth of the lophophore. The growth zones of the lophophore and those of the supporting lobate apparatus were thus entirely distinct from one another.



TEXT-FIG. 7. Lophophore and inferred feeding mechanism of *Lacazella* (A-C) and *Bactrynum* (D). A, dorsal valve of *Lacazella* with lophophoral filaments in contracted state, as illustrated by Lacaze-Duthiers (1861, pl. 3, fig. 1); B, C, lophophore of *Lacazella* in inferred feeding orientation, based on Lacaze-Duthiers' illustrations of opened shell (1861, pl. 1, figs. 2, 7) and on analogy with *Megathiris* (Atkins 1960); D, reconstruction of brachial axis and filaments of *Bactrynum*, shown as section through two lateral lobes; note brachial axis (dark stippled) in groove in surface of dorsal valve (light stippled), with filaments arching over 'lateral septa' to form 'tunnels'; arrows show water currents and food currents.

FEEDING MECHANISMS

Some elements of the foregoing reconstructions of the lophophore are necessarily conjectural. But of the assumptions made, only three are essential for the validity of the functional interpretation given here: (a) that the basic anatomy of the lophophores of *Thecospira* and *Bactrynum* resembled that of all living brachiopods; (b) that their basic orientation relative to the body likewise resembled that of all living brachiopods; and (c) that in each genus the grooves in the skeletal apparatus bore single rows of the brachial axis, so that the lophophore was spirolophous in *Thecospira* and ptycholophous in *Bactrynum*. For the reconstruction of the feeding mechanisms, i.e. of the lophophores

in operation, one further assumption is necessary: (*d*) that the basic functional mechanisms of the lophophores were normal, i.e. that they resembled those of all living brachiopods (Rudwick 1962, and references therein). These assumptions of anatomical and physiological uniformity are not of course capable of direct proof. But it is methodologically a sound procedure to begin by testing them indirectly, by determining whether they give a consistent and intelligible explanation of the morphology of the fossils. Only if they fail to do so should departures from uniformity be postulated (cf. Rudwick 1964).

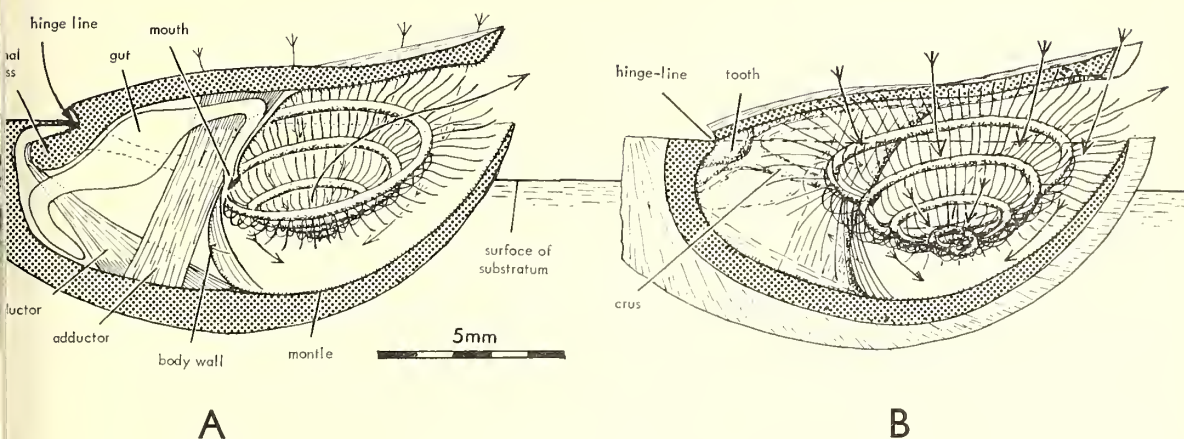
For effective ciliary filter-feeding in a brachiopod, it is essential that the tips of all the filaments (except those projecting at the gape and delimiting the apertures) should touch the mantle surface or the tips of other filaments. Only by so doing can the lophophore divide the mantle cavity into separate inhalant and exhalant chambers and thereby prevent wasteful re-circulation and re-filtering of the water (Rudwick 1960). The possible ways in which a pair of linear brachia can divide the mantle cavity is limited by inherent topological considerations, and only three essentially different arrangements are known in living brachiopods (Rudwick 1962). The spiroloph and ptychloph, here posulated for *Thecospira* and *Bactrynum* respectively, are two of these three known arrangements.

Current-system of Thecospira. A topological argument developed for the reconstruction of any spiroloph (Rudwick 1960) can be used to infer the attitude of the filaments in *Thecospira*. Inhalant and exhalant chambers could not be isolated unless the filaments on the spiral brachia touched the brachial axis of either the next proximal or the next distal whorl. But on the latter assumption the filaments on the first or most proximal whorl would have touched the axis of the second whorl, and no filaments would have been available to bridge the gap between the axis of the first whorl and the dorsal mantle. Therefore only the former alternative is feasible.

On the distal whorls, the tips of the filaments would thus have touched the brachial axis of the next proximal whorl; on the medial part of the proximal whorl they would have touched either the tips of the corresponding filaments on the other brachium, or else the ventral mantle; anteriorly on this whorl, they would have passed across the gape, projecting freely as apertural filaments; and laterally they would have touched the dorsal mantle. Posteriorly, in the most proximal part of the lophophore, they would have touched the lateral body wall and finally the anterior body wall or ventral mantle (text-figs. 8, 9).

Only by this precise orientation of all the filaments could the spiroloph of *Thecospira* have divided the mantle cavity into separate inhalant and exhalant chambers; by no other arrangement is it topologically possible for this essential functional condition to have been met. Of the only two possible varieties of the spirolophous system, the orientation of the brachial lamellae thus shows that the interior of the spirals must have been an exhalant space, so that *Thecospira* must have operated the 'exhalant' or '*Spirifer*' type, which has also been inferred for most spiriferides (Rudwick 1960) and is known in the living *Discinisca* (Paine 1962).

The inhalant chamber in *Thecospira* would thus have comprised the ventral part of the mantle cavity, external to the spirals; while the exhalant chamber would have occupied the dorsal part, together with the interior of the spirals, and would also have included a narrow exhalant space between the proximal filaments and the body wall.



TEXT-FIG. 8. A. Reconstruction of *Thecospira*, lateral view, cut along median plane. Inhalant water (tailed arrows) is seen entering laterally and circulating around exterior of spiral brachium; exhalant water (tailless arrows) is seen emerging from interior of spiral and leaving mantle cavity by a median aperture. To clarify the current system, brachial axes are shown more slender, and filaments more widely spaced, than in reality. Digestive glands omitted.

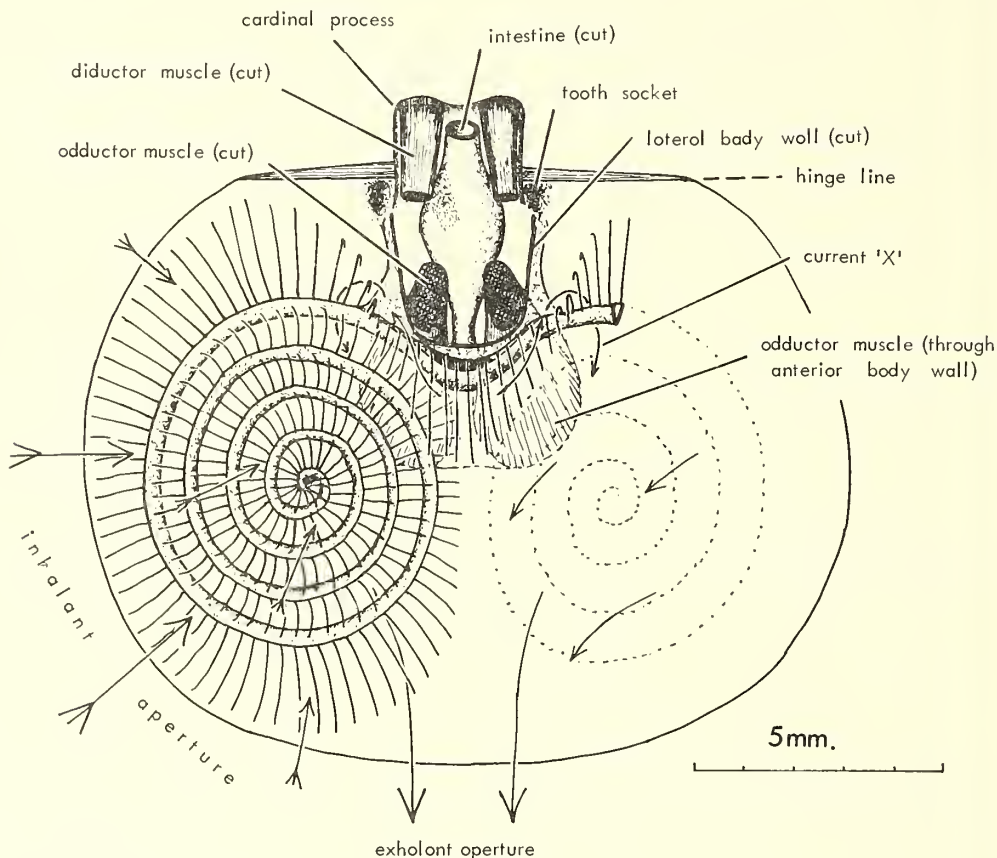
B. Similar reconstruction, with shell cut in plane parallel to median plane on right side, but with right brachium preserved intact (water currents are those that would operate with whole shell intact); showing crus embedded in lateral body wall, through which muscles and gut are faintly visible. For further explanation see text.

Given this orientation of the filaments, the current system of *Thecospira* follows necessarily (text-figs. 8, 9). Water must have entered the mantle cavity laterally, being drawn down into the inhalant chamber by the pumping action of the filaments removing water into the exhalant chamber. After being filtered between the filaments on the spirals, the water would have flowed as an exhalant current up the axis of each spiral, and then forwards to leave the mantle cavity medially. Water filtered by the most proximal filaments would have flowed along the narrow space between those filaments and the body wall, emerging to join the main exhalant current on either side of the dorsal part of the body wall (text-fig. 9, current 'X'): a similar current can be observed in living articulate (cf. Rudwick 1962, text-figs. 7c, 9a, c, 12b).

Thus the morphology of the brachidium of *Thecospira* is consistent with a ciliary feeding mechanism essentially similar to that of living brachiopods.

The rate at which a lophophore can pump water through a mantle cavity is roughly proportional to the total area of the filament-row. On a spirolophore, the rate is therefore approximately proportional to the area of the roughly conical surfaces which are formed by the spiral brachia when all the filaments are in their natural orientation. Thus in

a spire-bearing brachiopod the larger the conical 'framework' formed by each spiraliu, the greater the filtering capacity of the brachium must have been. For a shell of given size, the most effective arrangement of the spiralia would be that which most fully occupies the available space of the mantle cavity, while leaving sufficient space for the circulation of the water currents outside the spirals.



TEXT-FIG. 9. Reconstruction of *Thecospira*, ventral view of dorsal valve, and dorsal part of 'body', with lophophore (right brachium cut off near base to clarify course of exhalant currents). Other conventions as in text-fig. 8.

The observed arrangement of the brachidium in *Thecospira* approximates to this paradigm. The spiralia are so closely moulded to the available space that when the shell was closed the filaments must have been almost or quite in contact with the ventral mantle. When the shell opened, however, the brachidium and lophophore, being attached rigidly to the dorsal valve, would have been raised clear of the ventral mantle, thus allowing the circulation of water outside the spiral brachia.

At the degree of opening selected for illustration here (text-figs. 8, 9), the circulation

space outside the spiral brachia approximates to that observed outside the spirolophes of the living rhynchonellide *Notosaria* and the living *Crania* (Rudwick 1962, text-fig. 7; Atkins and Rudwick 1962, text-fig. 1). If the dorsal valve opened through a wider angle than that shown in this reconstruction, the same current system would have operated, except that the lateral inhalant apertures would have coalesced anteriorly, on the ventral side of the exhalant aperture, to form a single inhalant aperture.

The functional advantage of developing a brachial support for the spirolophe is not entirely clear. A possible explanation is that a calcareous support for the brachial axis takes up less space than the rather bulky hydrostatic and muscular skeletons seen in the spirolophes of living brachiopods (e.g. Atkins 1963, fig. 8A). Consequently the successive whorls of the spiral brachia can be set more closely together without substantially impeding the flow of water; and thus a greater area of filaments can be accommodated within a mantle cavity of given form and volume. But, on the other hand, this increased efficiency of the lophophore is obtained at the expense of having a supporting structure that is less flexible and more vulnerable to damage than is a hydrostatic skeleton. Thus, a spiral brachidium may on balance be advantageous in some circumstances; but, of course, it is only an available option in those brachiopods that have developed the power of resorption in the epithelia of the mantle.

Current-system of Bactrynum. In a schizolophe or ptycholophe the only effective arrangement of the filaments is for those in the indentations to be flexed abfrontally so that their tips are contiguous. Thus each indentation forms a 'tunnel' of exhalant water, blind-ended proximally but opening peripherally.

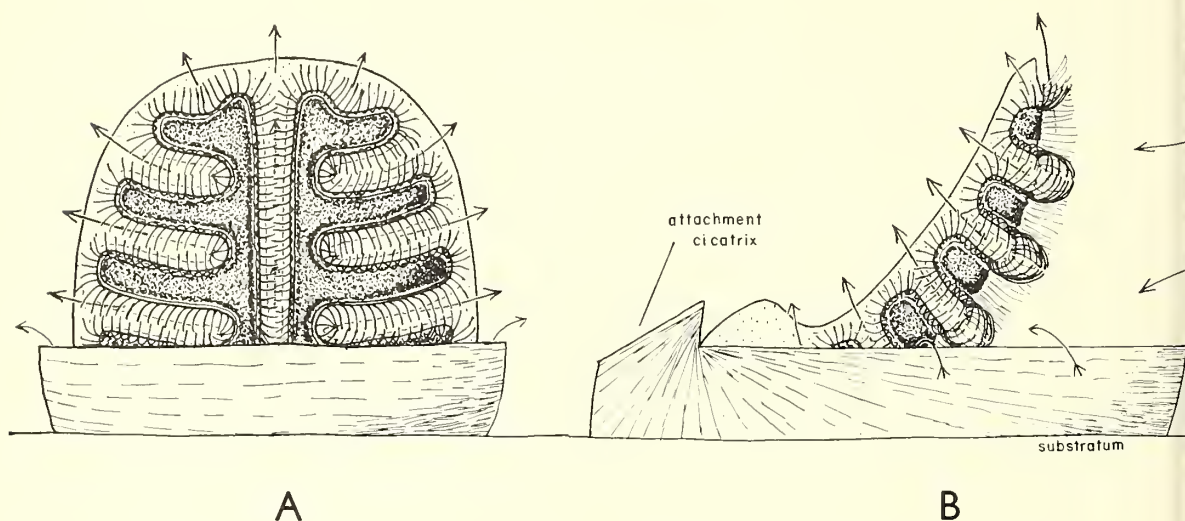
Such an orientation is in fact known in all living species in which schizolophes or ptycholophes have been observed in operation. In these lophophores the filaments are flexed abfrontally all along the brachial axis. In a schizolophe the tips of the filaments touch each other across the median indentation, forming a median 'tunnel' which is blind-ended posteriorly but open anteriorly; this has been observed in *Argyrothea* and *Pumilus* and in the schizolophous growth-stages of *Notosaria* and *Waltonia* (Atkins 1960, fig. 2; Rudwick 1962, fig. 6, 7a, 9a). The schizolophe of *Thecidellina* has not yet been described in operation. In a ptycholophe there are similar 'tunnels' in the lateral indentations as well; this has been seen in *Megathiris* (Atkins 1960, fig. 6). Lacaze-Duthiers (1861) only observed *Lacazella* with the filaments contracted frontally (text-fig. 7A), but their probable natural orientation can be inferred (text-figs. 7B, C) by analogy with *Megathiris*.

In all these schizolophes and ptycholophes the space near the dorsal valve surface is divided into two parts; the space corresponding to the lobes is filled with inhalant water, whereas the space corresponding to the indentations is filled with exhalant water. Water is filtered through the filament-row around the periphery of the lophophore, but also passes into the blind-ended tunnels in the indentations, from which it emerges peripherally (cf. Atkins 1960, fig. 6; Rudwick 1962, fig. 6).

The wide gape between the valve edges of *Megathiris* (and probably *Lacazella* also) is divided in effect into two apertures. The exhalant aperture extends all round the gape as a fairly narrow zone near the dorsal valve edge; the inhalant aperture occupies the remainder of the gape, nearer the ventral valve but not extending as far posteriorly. The apertures are separated only by the tips of the filaments around the periphery of the

lophophore. In principle there might be re-circulation around these apertural filaments; but in practice the wide opening of the shell exposes the periphery of the lophophore to sufficient external currents and turbulence to render any re-circulation insignificant.

It is reasonable to reconstruct the filaments of *Bactrynum* in a similar orientation, forming 'tunnels' across each of the indentations (text-fig. 7D). Then its current system would also have been similar (text-fig. 10). Water would have been drawn towards the dorsal valve surface, and would then have been filtered either through the filament-row around the periphery or else into the tunnels; within each tunnel an exhalant current would have flowed laterally or anteriorly to emerge near the edge of the valve. Thus in effect the part of the gape nearest the dorsal valve edge would have been an exhalant



TEXT-FIG. 10. Reconstruction of *Bactrynum* in feeding position, showing inferred orientation of filaments, and consequent paths of inhalant and exhalant currents. A, anterior view; B, lateral view.

aperture, and the rest of the gape a wide inhalant aperture. Unless *Bactrynum* lived in exceptionally still water there would have been little risk of any substantial re-circulation of the water.

As in *Thecospira*, therefore, the observed morphology of *Bactrynum* is consistent with a ciliary feeding mechanism essentially similar to that of living brachiopods.

On this interpretation *Bactrynum* developed the ptycholophous alternative to a greater degree of elaboration than in any living brachiopod. This may be related functionally to its greater size. Observations on living brachiopods of various species and at various growth stages suggest that the pumping capacity of filaments is roughly

constant, as might be expected of a property dependent on a mechanism (i.e. the ciliary action) operating on the cellular level (Rudwick 1962, p. 611). But the pressure difference (between inhalant and exhalant chambers or spaces) at which a lophophore can operate is limited by the ability of the slender and unfused filaments to withstand the pressure and remain in position. Therefore if a blind-ended tunnel formed from two apposed stretches of filament-row were below some critical width, the rate at which water was being pumped into the tunnel might exceed the rate at which it could escape down the tunnel, and the water might then force the filaments out of position and flow back into the inhalant space. On the other hand it is clearly advantageous to the efficiency of the whole ciliary feeding mechanism that each tunnel should be as narrow as possible without incurring the problem mentioned above: for only so can the maximum total length of filament-row, and hence the maximum filtering capacity, be accommodated within a shell of given size. There must, therefore, be some optimal width for the tunnels, which would be the same for any normal ptycholophe. Similarly, it is clearly advantageous that the inhalant 'troughs' between the exhalant tunnels should also be parallel-sided and of some uniform width, so that as many as possible can be provided in a given space.

Thus the entire form of a ptycholophe can be interpreted as a means of maintaining the maximum effective filtering capacity within a shell of limited size. Any ptycholophe is inherently limited by being attached throughout to the mantle, so that its elaboration to provide greater filtering capacity can only be in two dimensions, making the best use of the *area* of the dorsal valve surface (cf. Rudwick 1962, p. 611). The only means of lengthening an attached filament-row within such a limited area is to buckle it into lobes and indentations. But if there are also definite optimal widths for these lobes and indentations, the lophophore must be elaborated during growth by the sequential addition of new lobes and indentations to an initially simple schizolophe. Hence it is to be expected that the degree of elaboration of the ptycholophe should be directly related to the absolute size of the dorsal valve, both during the ontogeny of a single species and also among species of different adult sizes. It should thus show 'size-required allometry' (Gould 1966). This seems to be true of *Bactrynum* as far as the limited number of specimens allows such a conclusion (text-fig. 5); and a comparison with some thecideaceans (text-fig. 11) shows that they too have lobes and indentations of about the same size.

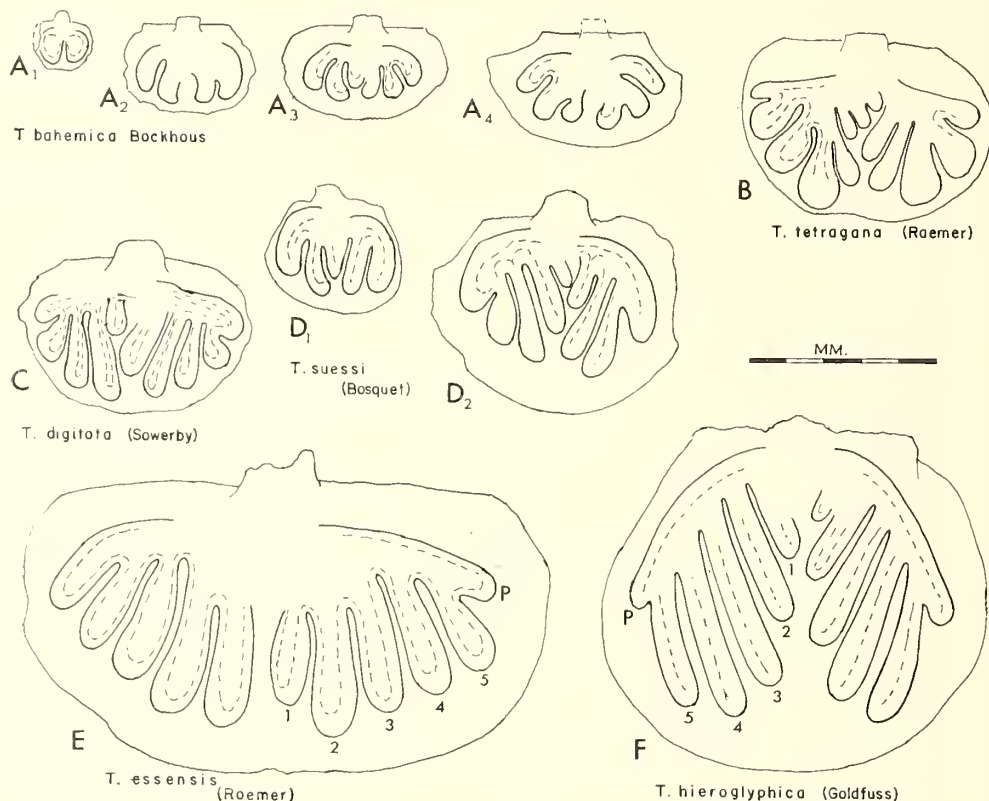
Unfortunately, quantification of this allometric relation is hardly possible, in view of the difficulties of estimating the size of the true 'body' of a brachiopod, as opposed to the size of its mantle and shell.

AFFINITIES AND EVOLUTION

Affinities of Thecospira. Williams (1953a) pointed out that *Thecospira* had such strikingly strophomenide characters that it could not be excluded from that group solely because of its possession of a spiral brachidium, the only character which suggested affinity with the spiriferides. *Thecospira* was therefore included within the Orthotetacea (now Davidsoniacea).

Like the davidsoniaceans of the Palaeozoic, *Thecospira* was cemented by the ventral valve during the earlier part of its life history; it has a strophic hinge-line, well-developed

teeth and sockets, and a large rectangular cardinal process. Most Palaeozoic davidsoniaceans (except the earliest) are pseudopunctate, but *Schuchertella* is said to be impunctate (Williams 1965, p. 408), and an apparently punctate structure has been reported in *Streptorhynchus* (Thomas 1958). Against this background of diverse shell structure, the existence of punctate, impunctate, and obscurely pseudopunctate species of *Thecospira* is consistent with an argument for affinity.



TEXT-FIG. 11. Drawings of the grooves and ridges on the dorsal valve of various species of *Thecidiopsis*, to show the uniformity of dimensions of the lobes. All $\times 5$; compare with *Bactrynum*, text-fig. 5. (Sources: A, Nekvasilova 1964, pl. XI, fig. 4, 6, 8; pl. XII, fig. 5; B-F, Backhaus 1959, B, pl. 5, fig. 4; C, pl. 4, fig. 2; D, pl. 7, fig. 1, 2; E, pl. 4, fig. 8; F, pl. 5, fig. 7.) Lobes of E and F marked with inferred order of development; compare text-fig. 6C. Scale represents 5 mm.

Thecospira is exceptional among davidsoniaceans in having an 'entire' (i.e. plane) pseudodeltidium (Williams 1965, p. H366), but this is a development that certainly occurred several times among the strophomeninids, and apparently related shells have a convex pseudodeltidium. Likewise it has lost all but a faint trace of the costellate shell surface characteristic of davidsoniaceans, but this too occurred in other strophomeninid groups (Williams 1965, p. H364). When the costellae are most clearly visible they show a pattern of increase by intercalation, as in other davidsoniaceans, and not by lateral branching. The pustular or spinule-bearing shell surface which apparently replaced the

costellae is not found, so far as I am aware, in any other davidsoniacean, and is more reminiscent of productaceans such as *Waagenoconcha*. But *Thecospira* lacks the larger tubular spines that seem to have been universal among the productaceans and strophalosiaceans.

The most important character distinguishing *Thecospira* from other davidsoniaceans is, of course, the spiral brachidium. But the unique structure of the lamellae suggests that the brachidium developed independently from those of the Spiriferida.

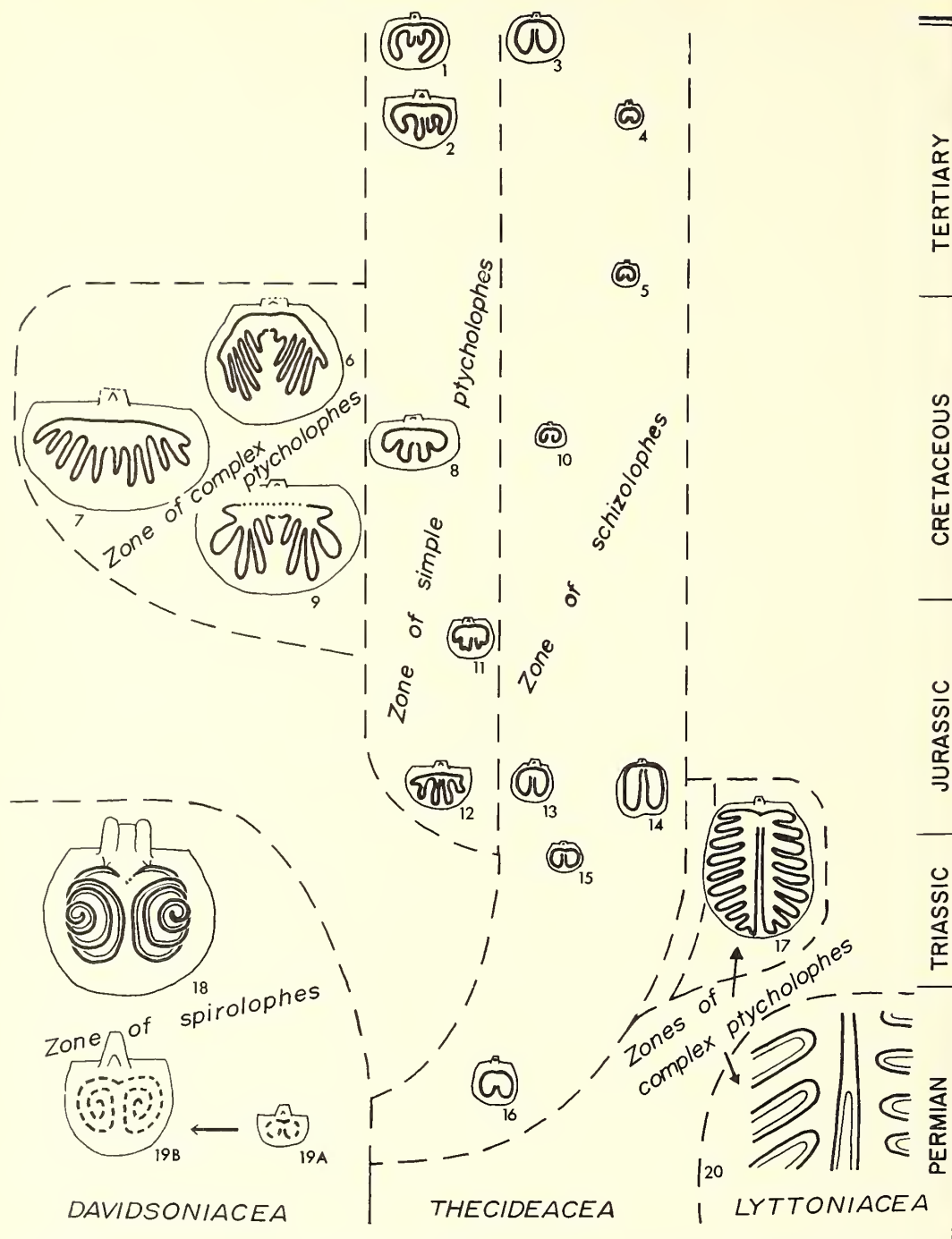
Spiral brachidia have recently been reported in *Cadomella* (Cowen and Rudwick 1966), which is generally regarded as related to the chonetaceans, so that there is now evidence that spiral brachidia evolved at least *twice* outside the Spiriferida. Even among the Spiriferida themselves spiral brachidia may have evolved more than once, the atrypaceans being in many respects closer to the rhynchonellides than to most other spiriferides (Copper 1965).

Palaeozoic davidsoniaceans probably possessed spirolophes supported by a hydrostatic or other 'soft' skeleton, for spiral impressions are known in *Davidsonia* itself. Davidsoniaceans existed in considerable abundance and variety even in Upper Permian time. The teeth of *Thecospira*, being unsupported by dental lamellae, suggest the Schuchertellidae or Orthotetidae as possible ancestors. The cardinal process and 'socket plates' have perhaps the greatest resemblance to those of *Streptorhynchus*; *Orthotetes* is another possible ancestor.

From some such Permian ancestor, the evolution of *Thecospira* would have involved (a) acquisition of brachidium (b) loss of convexity in pseudodeltidium and chilidium (c) obsolescence of costellae and (in some species) replacement by pustules, and possibly (d) loss of pseudopunctate structure and (in some species) acquisition of punctae. There is, however, no reason to suppose that these changes took place simultaneously. As already mentioned, the diversity of shell structure in *Thecospira* was foreshadowed in the Permian davidsoniaceans. Even the spiral brachidium may have evolved earlier than is yet apparent, and it might be worth examining Permian davidsoniaceans for any trace of the bases of crura. In any case, the evolution of *Thecospira* would not have involved any major changes in the relation of the shell to the substratum, in the hinge and musculature, or in the ciliary feeding mechanism. Only the supporting structures of the brachial axis would have changed, from a probably hydrostatic to a purely calcareous skeleton. As already suggested, there may have been an adaptive advantage in this change, in allowing a greater filtering capacity within a shell of given size.

The Koninckinidae, which have generally been regarded as abnormal Spiriferida, should probably now be placed with *Cadomella* as post-Palaeozoic descendants of the chonetaceans (Cowen and Rudwick 1966). Like *Thecospira*, the koninckinids are first known from Middle Triassic strata, but they are significantly different in the structure of the brachidium and many other characters. If this interpretation of koninckinids is correct, it implies that two relict strophomenide groups evolved spiral brachidia independently at about the same time, after most of the related 'normal' genera had become extinct.

Affinities of Bactrynum. As already mentioned, the affinities of *Bactrynum* have remained more controversial than those of *Thecospira*. Affinity to Lyttoniaceae and to Thecideaceae are interpretations that have been almost equally supported for many



TEXT-FIG. 12. Diagram to show inferred phyletic and functional relationships of *Bactrynum* and *Thecospira* to other brachiopods. Outlines of dorsal valves of representative species are shown at uniform

decades. The form of the lobate apparatus of *Bactrynum* has an immediate resemblance to that of the lytoniaceans. The strongly concave form of the dorsal valve gives it an especially close resemblance to *Oldhamina*. It is necessary, however, to examine these similarities critically, in order to assess their value as clues to affinity.

In a lytoniacean the highly modified dorsal valve ('internal plate' of Williams 1953b, 1965) has a pair of sub-parallel submedian primary lobes, from which secondary lobes branch laterally. Between the lobes are lateral indentations and a single median indentation. The degree of symmetry is variable, but in *Oldhamina* and *Leptodus*, for example, it is as great as in *Bactrynum*. In such genera as these, there is also an obvious approach to uniformity in the width of the lobes and of the indentations. The mode of growth of the lobes can be inferred, by analogous reasoning, to have been similar to that of *Bactrynum*, with the secondary lobes extending laterally, while each primary lobe extended forwards and periodically 'budded off' a new secondary lobe. This is confirmed by the evidence of the growth-lines on the lobes. The similarities even extend to the detailed morphology, for the inner side of the dorsal valve of lytoniaceans has a contiguous ridge and groove (the ridge being external to the groove) running around the edge of the lobes and indentations, while the area enclosed by the groove is often pustular in appearance (Pl. 68, fig. 10; see also Stehli 1956, pl. 41, fig. 3; Williams 1965, fig. 393, 3d).

But the differences between the lobate apparatus of *Bactrynum* and the dorsal valve of a lytoniacean are as striking as the resemblances.

The strophic hinge and articulation of *Bactrynum* are apparently quite normal, and are certainly unlike the highly aberrant hinge structures of the lytoniaceans. The dorsal valve of *Bactrynum* is a thick massive plate, whereas that of a lytoniacean is exceptionally thin and delicate. More significantly, the dorsal valve of *Bactrynum* has a normal 'entire' outline, whereas that of a lytoniacean is highly indented and corresponds to the course of the lobed ridge. It is true that its indented outline is often modified by 'bridges' of shell material across the indentations, either occasional as in *Oldhamina* (cf. Williams 1965, fig. 293, 2b), confined to the median indentation as in *Gubleria* (Termier and Termier 1960), or regularly across all the indentations as in *Coscinophora* (cf. Williams 1965, fig. 393, 1a, 1c). The inner ends of the posterior

magnification ($\times 2$), with course of brachial axes (reconstructed from brachial grooves or brachidial lamellae) marked in thicker black lines (hatched where reconstruction is tentative). Note fairly uniform dimensions of lobes of Thecideacea (1-17) and spiralia of *Thecospira* (18) in contrast to much larger lobes of Lytoniaceae (20). Variations in adult body size are indicated approximately by positions on horizontal scale, smallest species being roughly central. (If space allowed, the lytoniacean (20) would be much further to right.) Stratigraphical horizons of species indicated approximately against Geological Society time-scale (*Quart. J. geol. Soc. Lond.* **120S**, 260-2). Broad outline of suggested phylogeny shown by functional 'zones' based on type of lophophore in *adult* stage: specific phyletic pathways are not given. For further explanation see text. Key to genera: THECIDEACEA: 1. *Lacazella*; 2. *Glazewskia*; 3-5. *Thecidellina*; 6. *Parathecidea*; 7-9. *Thecidiopsis*; 10. *Bifolium*; 11. *Glazewskia*; 12. *Eudesella*; 13. *Elliottina*; 14. *Davidsonella*; 15. *Moorellina*; 16. *Cooperina*; 17. *Bactrynum*; DAVIDSONIACEA: 18. *Thecospira*; 19. A Permian davidsoniacean (based on *Diplanus*), with (A) juvenile stage with inferred schizolophe, and (B) adult with inferred spirolophe. LYTONIACEA: 20. *Leptodus* (Fragment only). (Sources: 2, Pajaud 1965; 4, Thomson 1915; 5, Toulmin 1940; 6-9, Backhaus 1959; 10, Nekvasilova 1964; 11, Glazewski and Pajaud 1965; 16, Termier, Termier and Pajaud 1966; 1, 3, 12-15, 17-20 original.)

indentations may also be filled up progressively, as in *Leptodus* (cf. Williams 1965, fig. 393, 3d). But in no lytoniacean were the indentations completely filled in: even in *Coscinophora* gaps of uniform length were maintained between the regularly spaced 'bridges' across the indentations. As Sarycheva (1964) has pointed out, Stehli's (1956) suggested derivation of *Bactrynum* from *Coscinophora* is therefore improbable.

The indented edge of the dorsal valve of lytoniaceans rests on a series of septa rising from the floor of the ventral valve. The interior of the ventral valve of *Bactrynum* is not well known, but it certainly has no such septa rising to make contact with the lobate apparatus on the dorsal valve (text-fig. 2B; Pl. 68, fig. 9).

Another difference of great importance is that of absolute size. The lobes and indentations on a lytoniacean are nearly three times as large (in linear dimensions) as those of *Bactrynum* (text-fig. 12; Pl. 68, compare fig. 10 with fig. 1). This difference is independent of the absolute size of the whole shell, since in both groups the width of the lobes and the width of the indentations were clearly kept more or less constant during growth. As Gould (1966, p. 604) suggests, such a difference should draw attention to a probable adaptive discontinuity between the groups concerned.

The morphology of lytoniaceans is so abnormal that any reconstruction of their feeding mechanism on grounds of analogy alone would be hazardous. Only a full functional analysis of their morphology will give rational grounds for any such reconstruction. In the meantime, it should not be assumed that their feeding mechanism was necessarily the same as that of *Bactrynum*. In particular the very thin and delicate dorsal valve, recessed within a more robust ventral valve, and the persistently maintained slots or perforations between the lobes of the dorsal valve, suggest a significantly different functional organization; and the much larger dimensions of the lobes and indentations point to the same conclusion.

On the other hand it is probable that the groove running round the lobes and indentations bore a brachial axis as in *Bactrynum*, and that the lophophore therefore was a Ptychopore. If this is correct, the same topological considerations could have been responsible for the very similar arrangement and mode of growth of the lobes. The over-all similarity could, therefore, be due to simple functional parallelism.

There is now no good evidence for the survival of true lytoniaceans after the end of the Permian period. The large stratigraphical gap between the last undoubted lytoniaceans in the Dzhulfian (late Permian), and *Bactrynum* in the Rhaetian (late Triassic), is therefore no longer a problem.

A much closer comparison can be made between *Bactrynum* and the thecideaceans. In both, the dorsal valve is a massive plate with a thickened sub-marginal rim and 'entire' outline. The ventral valve is cemented to the substratum, at least in earlier growth-stages. The rectangular cardinal process of *Bactrynum*, with flanking sockets and socket plates, is closely similar to the cardinalia of thecideaceans. The shell surface of thecideaceans has no radial ornament. The hinge is strophic, with a low dorsal interarea and higher ventral interarea.

Many other characters of *Bactrynum* can be matched among the earlier thecideaceans of the Lower Jurassic. Thus *Davidsonella* has already been reported as pseudopunctate (Elliott 1965), and there is a similar obscurely pseudopunctate structure in *Moorellina leptenoides* (Deslongchamps).

The cardinal process and sockets are similar to those of *Bactrynum*, and lateral to

the cardinal process is a pair of elliptical areas similar to the postulated lateral adductor scars of *Bactrynum*. The ventral valve is generally strongly convex, and the dorsal valve may be concave as in *Bactrynum* (e.g. *Davidsonella sinuata* (Deslongchamps)). There is a similar lobed ridge and groove in *Endesella* (Pl. 68, fig. 3). The area within the groove is generally pustular (Pl. 68, figs. 3, 7, 8). In *Davidsonella* pustules are highly developed (Pl. 68, figs. 4, 5), but do not appear to be separate spicules as implied in the *Treatise* description (Elliott 1965, p. H859). Posteriorly the ridge projects across a postero-median cavity, often as a complete 'bridge', which is quite distinct from the 'socket plates' (Pl. 68, fig. 4). The median indentation of the ridge may project posteriorly as a distinctly doubled spur or spike closely resembling that of *Bactrynum* (Pl. 68, figs. 4-6).

In thecideaceans there is, as already mentioned, a clear approximation to a uniform width for the lobes and for the indentations, both in the different growth stages of a species and between different species; and these uniform dimensions are closely comparable to those of *Bactrynum* (compare text-fig. 11 with text-fig. 5; also Pl. 68, compare figs. 3-5, 7, 8 with fig. 1). This suggests a common feeding mechanism for *Bactrynum* and thecideaceans, with 'tunnels' of exhalant water stabilized at the optimum dimensions inherent in any normal (i.e. non-lyttoniacean) ptycholophous system.

The chief difference between the lobes of *Bactrynum* and those of the thecideaceans lies in their arrangement. In genera with several lobes the lobes project anteriorly or antero-medially, and never laterally (text-fig. 11). It can, however, be inferred that they grew in the same manner as that postulated for *Bactrynum*. The difference is that the primary lobe of thecideaceans is that *furthest* from the mid-line, not that nearest the mid-line. The primary lobe extends parallel to the postero-lateral sector of the valve edge; the secondary lobes project anteriorly or antero-medially from it, and must have been 'budded' from it serially, the postero-median lobes being the oldest (text-figs. 6C-D). Expressed another way, the secondary lobes were budded from the medial side of the primary lobe in thecideaceans, but from the lateral side in *Bactrynum*. Beginning from a schizolophous stage, these are, in fact, the only two distinct ways in which the number of lobes can be increased (without involving an unlimited amount of shift in the absolute positions of all the lobes). As already shown, it appears that *Bactrynum* actualized one of these alternative possibilities, with secondary lobes being formed serially on the lateral side of each primary lobe; whereas the thecideaceans actualized the other alternative, with secondary lobes being formed serially on the medial side of each primary lobe (in some thecideaceans the budding pattern may have been irregular—see text-figs. 11A-C).

These alternatives, though topologically equivalent, are probably not equal in functional efficiency. On the first alternative (*Bactrynum*) all the secondary lobes project laterally, and hence all the 'tunnels' (except the median one) opened laterally. On the second alternative (Thecideacea) all the secondary lobes project antero-medially, anteriorly, or at most antero-laterally, so that all the 'tunnels' open around the anterior part of the gape. In terms of the current systems, the greatest outflow of exhalant water would be, on the first alternative, in the lateral part of the gape, and on the second, in the anterior part. But the area available to act as exhalant aperture is limited laterally by the degree of separation of the valve edges, whereas anteriorly the much wider total gape can be divided between inhalant and exhalant apertures simply by an appropriate

orientation of the apertural filaments. In other words it would seem simpler to ensure an unimpeded outflow of exhalant water on the second alternative than on the first. This suggests a possible adaptive advantage in favour of the thecideaceans, which may be reflected in their longer range and greater diversity and abundance.

It is interesting that within the lyttoniaceans there are genera (e.g. *Paralyttonia*, *Rigbyella*) with forwardly projecting lobes like those of the thecideaceans, as well as the better-known genera (e.g. *Oldhamina*, *Leptodus*) with laterally projecting lobes like those of *Bactrynum*. This fact was used by Wanner (1935) as an argument for affinity between lyttoniaceans and thecideaceans (including *Bactrynum*). He maintained that any other interpretation would involve postulating a *double* convergence. But the present analysis of the growth of ptycholophes implies on the contrary that the parallel development of both alternative arrangements of the lobes is by no means improbable.

These similarities together make a strong case for affinity between *Bactrynum* and Thecideacea. Indeed, in my opinion there is now no difference warranting supra-familial recognition. I therefore suggest that *Bactrynum*, while retaining its family Bactryniidae in recognition of the distinctive form of its lobate apparatus, should be assigned to the Thecideacea.

In phylogenetic terms *Bactrynum* can best be regarded as a derivative of small and simple schizolophous thecideacean ancestors. Such species are known in the Permian (*Cooperina*) and Rhaetian (e.g. *Moorellina*), and are probably represented in intermediate strata among the poorly known Triassic '*Thecidea*' spp. From some such ancestor, *Bactrynum* could have evolved allometrically by elaboration of the schizolophe into a ptycholophe and by concurrent increase in absolute size. Later ptycholophous forms, such as *Eudesella* in the Lower Jurassic, utilized the other alternative arrangement of lobes, and therefore probably evolved independently from schizolophous forms. *Bactrynum* might, however, have left some schizolophous descendants by neoteny; the pseudopunctate *Davidsonella*, for example, might have had such an origin.

Without attempting to reconstruct the detailed course of phylogeny in the Thecideacea, the functional analysis given here leads to an interpretation in terms of 'functional zones' (text-fig. 12). Each 'zone' represents the utilization of one possible mode of organization of the lophophore, without any necessary effect on the mode of life of the whole organism; functional zones are thus not synonymous with adaptive zones. Using this concept, it would seem that from the earliest thecideacean (*Cooperina*) onwards, there has always been a 'zone of schizolophes', occupied by species small enough for a schizolophe to be an adequate form for the lophophore. At certain times there have also been species which, by utilizing one or other ptycholophous arrangement, were able to increase in absolute size and evolve into 'zones of ptycholophes'. Gould (1966) has already cited some thecideaceans as an example of such 'size-required allometry'. Such species would, of course, have traversed the 'zone of schizolophes' during ontogeny, as, for example, *Lacazella* is known to do at the present day. I have made a somewhat arbitrary distinction between 'zones of simple ptycholophes', containing species with no more than three pairs of lobes, and 'zones of complex ptycholophes', containing species with larger numbers of lobes. The 'envelopes' outlining the zones on text-fig. 12 are merely to show the limits of known species in each zone: they do not imply that any zone was in any sense unavailable at other times, nor that all the specimens in a given zone are closely related to each other (e.g. *Eudesella* in the Lower Jurassic may have

evolved from schizolophous ancestors independently from the much later, Cretaceous, ptycholophous species).

Affinities of Thecideacea. Further discussion of the affinities of *Bactrynum* thus involves the question of thecideacean affinities. *Lacazella* and its fossil relatives formed an important element in the earlier concept of the 'Protremata', and underlying this was the belief that the Thecideacea were related to the brachiopods now grouped together as Strophomenida. More recently, however, this early view has been regarded as doubtful, and an affinity with the Terebratulida or Spiriferida has been favoured (Williams and Rowell 1965).

In this interpretation undue weight has perhaps been given to the fact that most Thecideacea are punctate. But it is now recognized that the punctate structure must have evolved independently several times during the history of the Brachiopoda (Williams and Rowell 1965, p. H68; Wright 1966). Therefore the punctation of Thecideacea is not by itself a reliable criterion of affinity to the Terebratulida or punctate Spiriferida. The existence of diverse shell structures among the earlier Thecideacea increases the likelihood that punctation has evolved independently in this group.

Two other important characters of Thecideacea, their cementation and their lobed brachial grooves, find no parallel among Spiriferida or Terebratulida. There is now no authenticated case of cementation attachment in any articulate brachiopod outside the Strophomenida; for Dagus (1965) has justly thrown doubt on *Thecocyrtella*, and *Bittnerula* is now known to have a pedicle foramen (Cowen and Rudwick 1967). The cemented attachment of Thecideacea is, therefore, strong evidence against any but a strophomenide affinity. Linked with the possession of cementation is the fact that Thecideacea have a pseudodeltidium and no pedicle foramen; and their cardinalia cannot be matched closely among terebratulides or spiriferides. The brachial supporting structures of Thecideacea, with the brachial axes in grooves excavated in the dorsal valve surface, are entirely different from any of the varied spiral and looped brachidia of Spiriferida and Terebratulida, all of which are composed of calcareous lamellae growing independently from the dorsal valve floor, though attached to the cardinalia and also (in some forms) to septa.

A far stronger case can be made for affinity between the Thecideacea and the Strophomenida. Of strophomenide brachiopods, the Davidsoniacea show the greatest resemblances to the Thecideacea. Both groups have cementation attachment and therefore no pedicle foramen, and both lack the tubular spines of chonetoids and productoids. Both have strophic hinges, with strong articulation flanking a fairly massive cardinal process which is generally covered by a convex pseudodeltidium.

This conclusion would be given taxonomic recognition by the assignment of the Thecideacea to the Strophomenida. Their possession of brachial grooves and related structures, implying schizolophous or ptycholophous but never spirolophous lophophores, their lack of costellate ornament, and their generally (but not universally) punctate shell structure are collectively sufficient grounds for retaining them as a superfamily distinct from the Davidsoniacea.

Until recently the Thecideacea were unknown before the Rhaetian (Elliott 1965); but with the discovery of the simple but true thecideacean *Cooperina* in the Word Formation (Upper Permian) of Texas (Termier, Termier, and Pajaud 1966), it is now

clear that the ancestors of the group must be sought among Lower Permian or even earlier davidsoniaceans. These, like the Devonian *Davidsonia* itself, probably had spirolophous lophophores supported only by a hydrostatic skeleton or by muscular and connective tissue. By analogy with living brachiopods, most Permian davidsoniaceans were almost certainly too large for a schizolophe to have been adequate for their needs; but like all living spirolophous species they would have passed through a schizolophous stage early in ontogeny while they were still small in size. In the light of these functional considerations a neotenous origin for the Thecideacea seems most probable. Only the development of a sessile schizolophe, accommodated in a groove in the dorsal valve, would have been required to convert a small and young davidsoniacean into a true thecideacean (text-fig. 12).

CONCLUSIONS

If the foregoing arguments are correct, the great Palaeozoic order of Strophomenida, which suffered a drastic degree of extinction at about the end of the Permian period, survived into the Mesozoic only as three groups of small, rare, and inconspicuous brachiopods. One group was the Koninckinidae, modified descendants of the Chonetacea (Cowen and Rudwick 1966). The second group consisted of small and simple davidsoniaceans together with *Thecospira*. The spiral brachidium of the latter genus may have evolved at about the same time (early or middle Triassic) as the parallel development in the Koninckinidae, both being independent of the spiral brachidium of the Spiriferida. The brachidium of *Thecospira* may have increased the efficiency of the pumping action of its lophophore, but did not entail any essential change in its ciliary feeding mechanism, or in the exhalant spirolophous current system by which that mechanism operated. Apart from its spiral brachidium *Thecospira* was functionally similar to more 'normal' davidsoniaceans. The third group, the Thecideacea, was already in existence even before the end of the Permian, and was probably derived by neoteny from the davidsoniaceans. In late Triassic time *Bactrynum* evolved from some small and simple thecideacean by elaboration of a schizolophe into a ptycholophe and by corresponding increase in size. This 'size-required allometry' involved no essential change in its ciliary feeding mechanism, but its concavo-convex shell form adapted it to a free-lying mode of life. *Bactrynum* itself became extinct at the end of the Triassic, though some neotenous descendants may be represented among the varied Thecideacea of the Lower Jurassic. These also included a new and independent development of ptycholophous forms (*Eudesella*). The Thecideacea survived thereafter, though inconspicuously, up to the present day. On this interpretation the Strophomenida are not yet extinct.

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M. J. S. RUDWICK
Department of Geology
Sedgwick Museum
Cambridge

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UPPER CRETACEOUS COCCOLITHOPHORIDS FROM ZULULAND, SOUTH AFRICA

by RICHARD N. PIENAAR

ABSTRACT. A detailed study of some Upper Cretaceous calcareous nannoplankton of Zululand was undertaken, utilizing the optical as well as the electron microscope. Nine new species belonging to five genera are described as viewed in the electron microscope. These are *Coccolithus cribosphaerella*, *Coccolithus zuhensium*, *Cyclolithus zuhua*, *Discolithus cristallinus*, *Discolithus rhabdosphaericus*, *Discolithus spiralis*, *Maslovella africana*, *Maslovella blackii*, and *Maslovella pulchra*. Using the sequential occurrence of the coccoliths through the top 800 ft. of 'Zululand Oil Exploration' Borehole 'A' the age was determined as being Cretaceous Maestrichtian.

THE material on which this study was based was supplied by the Anglo Transvaal Consolidated Investment Company of South Africa. It belongs to part of this company's oil prospecting project and is from Borehole 'A' drilled near Lake Sibaya, Zululand, South Africa.

The method used to extract and prepare the coccoliths for observation under both the optical as well as the electron microscope are similar to those described by Pienaar (1966).

All samples are housed in the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, while the prepared slides and electron micrographs are housed in the Department of Plant Biology, University of Natal, Durban, South Africa.

TAXONOMIC PROBLEMS

It has been shown by numerous workers in this field that the systematics of this group of algae is in a state of turmoil. This has arisen mainly out of the fact that there have been many approaches to this field of study. The use of phase contrast, polarizing, and ordinary optical microscope as well as the electron microscope have resulted in confusion within the group because these algal remains appear so completely different when viewed under the different microscopes.

It has been shown that the only satisfactory way to study this group systematically, is by utilizing the electron microscope which with its high power of resolution reveals the detailed structure of the coccoliths. This is vitally important as the systematics of the Coccolithophoridae is based on hard-part morphology; I do not suggest that the optical microscope be abandoned, and have in fact stressed (Pienaar 1966) that it is invaluable in the stratigraphic application of the group.

In the present report no attempt has been made to place the coccoliths under any hierarchical systematic framework. I consider it premature to do so until there is a good collection of electron micrographs available, and for this reason the coccoliths are described in alphabetical order.

[Palaeontology, Vol. 11, Part 3, 1968, pp. 361-7, pls. 69-71.]

DESCRIPTIVE TERMINOLOGY

Distal shield. Shield which is the furthest away from the point of attachment of the coccolith to the coccosphere, and is always convex.

Longitudinal axis. Line joining the two longitudinal poles.

Longitudinal poles. Situated at each end of the longitudinal axis of the theoretical ellipse that contains the coccolith.

Plates. Elements which comprise the proximal and distal shields; they vary from being wedge-shaped to rectangular in outline.

Pore. Region where there are no crystals of calcium carbonate, usually within the central area of the coccolith.

Proximal shield. Part of the coccolith which is in direct contact with the coccosphere; always concave.

Shield. Main structural element of a coccolith, always composed of plates.

Shield area. Width of the shields when the coccolith is seen in plan view.

Transverse axis. Line joining the two transverse poles.

Transverse poles. Situated at each end of the transverse axis of the theoretical ellipse that can contain the coccolith.

SYSTEMATIC DESCRIPTIONS

Genus COCCOLITHUS Schwarz 1894

Coccolithus cribosphaerella sp. nov.

Holotype. Plate 70, figs. 4, 5.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1382, depth 280 ft.; Cretaceous.

Diagnosis. Elliptical placoliths composed of two well-developed shields; distal shield larger, convex, composed of 21–22 plates. The exact detail of the smaller proximal shield is not known. The central area is sculptured with numerous pores aligned parallel to the longitudinal axis of the ellipse.

Description. The scalloped outline is due to the overlapping plates of the distal shield. The proximal shield is presumed to be similarly composed. The central area is sculptured

EXPLANATION TO PLATE 69

Figs. 1, 5. *Maslovella blackii* sp. nov. non-replicated. 1, $\times 28,000$. 5, $\times 10,700$.

Fig. 2. *Discolithus cristallinus* sp. nov., non-replicated; $\times 21,660$.

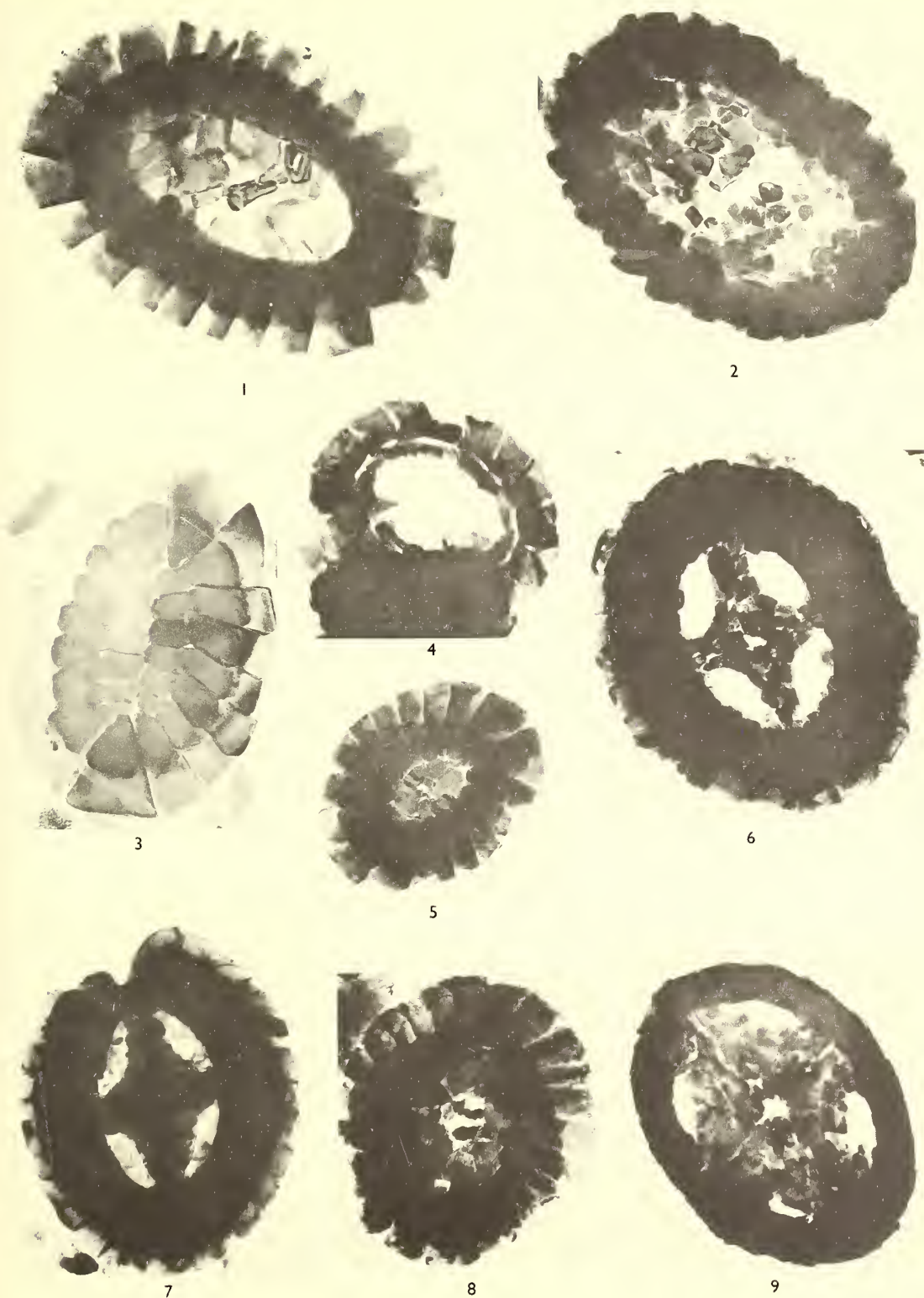
Fig. 3. *Maslovella pulchra* sp. nov., non-replicated; $\times 27,000$.

Fig. 4. *Cyclolithus zulua* sp. nov. non-replicated; $\times 13,330$.

Figs. 6, 7. *Coccolithus zuluensium* sp. nov., non-replicated. 6, $\times 13,330$. 7, $\times 13,750$.

Fig. 8. *Maslovella africana* sp. nov., non-replicated; $\times 12,850$.

Fig. 9. *Discolithus rhabdosphericus* sp. nov., non-replicated; $\times 13,125$.



PIENAAR, Cretaceous coccolithophorids

with 3–5 rows of pores aligned parallel to the longitudinal axis of the ellipse; the pores vary from circular to hexagonal in shape.

Size. Longitudinal axis, 4.5–6.0 μ . Transverse axis, 3.1–4.8 μ . Width of shield area, 0.75–1.0 μ .

Remarks. This coccolith is well represented in the assemblages studied. The pore size is variable. Stradner (1961) described *Coccolithus opacus* which resembles the South African species and could well be a related form.

Coccolithus zuluensium sp. nov.

Holotype. Plate 69, figs. 6, 7.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1388, depth 330 ft.; Cretaceous.

Diagnosis. Elliptical coccolith made up of two well-developed shields; distal shield larger. The central area is spanned by two cross-bars which widen centrally and correspond to the axes of the ellipse.

Description. The distal shield is composed of 27–29 overlapping plates. The longitudinal polar plates are wedge-shaped and are larger than the remaining rectangular plates. The proximal shield is similar in construction to the distal shield.

The central area is the characteristic feature of the species; the cross-bars are composed of calcium carbonate crystals arranged in an irregular manner.

Size. Longitudinal axis, 3.25–4.4 μ . Transverse axis, 2.3–3.7 μ . Width of shield area, 0.8–1.0 μ .

Remarks. The coccoliths grouped together in this species resemble *Discolithus rhabdosphaericus* sp. nov. but differ in that they have a proximal and a distal shield and lack a central boss. The species is assigned to the genus *Coccolithus* because of the two-shielded nature. It has been noticed that during the course of the study of the South African Coccolithophorids that the members belonging to the genus *Coccolithus* usually possess large wedge-shaped polar plates.

Genus CYCLOLITHUS Kamptner 1948

Cyclolithus zulu sp. nov.

Holotype. Plate 69, fig. 4; Plate 70, fig. 1.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1382, depth 280 ft.; Cretaceous.

Diagnosis. Elliptical coccolith composed of a single shield abutting against a raised central rim. The shield is made up of 16–17 plates.

Description. The 16–17 plates are rectangular and overlap slightly. Towards the central area is a raised rim, against which the plates abutt. The raised portion is levigate and devoid of any sculpture.

Size. Longitudinal axis, 4.4–6.0 μ . Transverse axis, 3.6–4.1 μ . Width of shield area, 0.9–1.0 μ .

Remarks. On first impression this specimen appears to have two shields but on closer examination the second shield is seen to be a slightly raised rim with practically no plate structure. Because of its one-shielded nature and the central area devoid of any sculpture, the specimens are placed in the genus *Cyclolithus* Kamptner 1948.

Remarks. Under the Botanical Code of Nomenclature, the name *Discolithus* is retained for these algal fossils (cf. Loeblich and Tappan 1963).

Genus DISCOLITHUS Kamptner 1948

Discolithus cristallinus sp. nov.

Holotype. Plate 69, fig. 2; Plate 70, fig. 2.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1382, depth 280 ft.; Cretaceous.

Diagnosis. Elliptical one-shielded coccolith composed of 24–40 overlapping plates. The central area is infilled with crystals of calcium carbonate arranged in an irregular order.

Description. The average number of plates is between 28 and 30.

Size. Longitudinal axis, 2.4–2.75 μ . Transverse axis, 1.4–7.0 μ . Width of shield area, 0.25–0.45 μ .

Remarks. Occasionally specimens of *Discolithus cristallinus* were found with a distinct row of crystals following the outline of the central area. Their appearance was almost like the beginning of a second shield. In addition some forms have larger crystals of calcium carbonate covering the smaller crystals. This species is easily recognized by its single shield and the infilled central area.

Discolithus rhabdosphaericus sp. nov.

Holotype. Plate 69, fig. 9; Plate 71, figs. 1, 2, and 6.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1382, depth 280 ft.; Cretaceous.

Diagnosis. Elliptical one-shielded coccolith composed of 35 overlapping plates. The central area is spanned by a solid parallelogram-like structure, the diagonals of which correspond with the axes of the ellipse.

Description. The sides of the parallelogram are concave and each composed of six plates. The diagonals are raised and unite in the centre to form a boss which is perforated by an axial pore. The proximal surface of the coccolith is markedly concave and no central

EXPLANATION TO PLATE 70

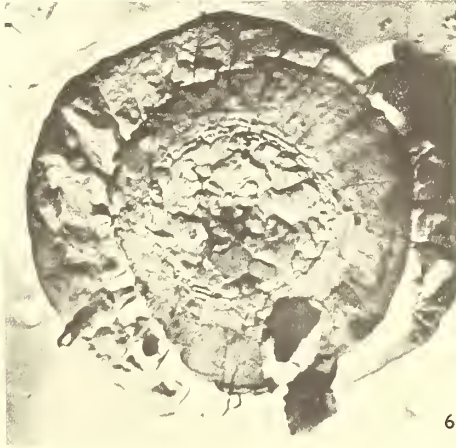
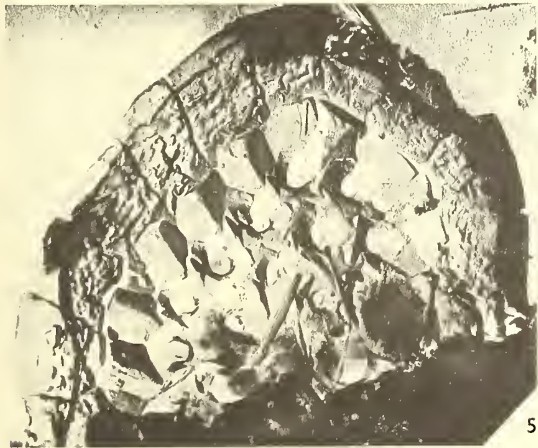
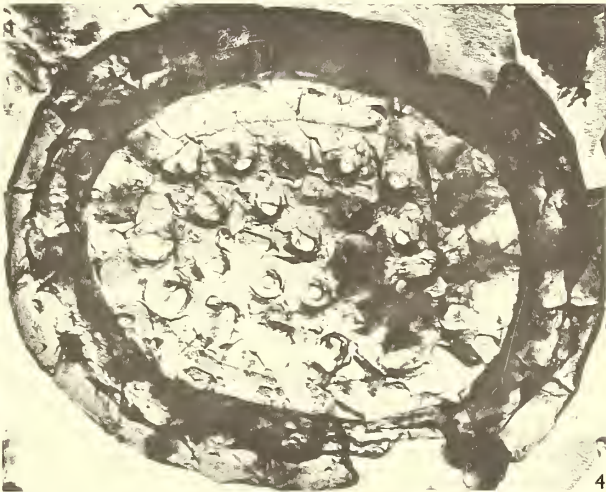
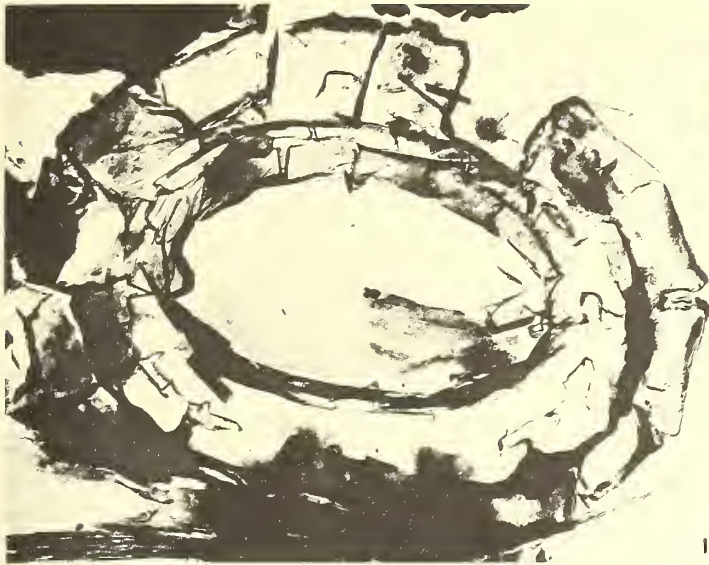
Fig. 1. *Cyclolithus zulua* sp. nov., replicated; $\times 30,000$.

Fig. 2. *Discolithus cristallinus* sp. nov., non-replicated; $\times 22,000$.

Fig. 3. *Discolithus spiralis* sp. nov., replicated; $\times 12,000$.

Figs. 4, 5. *Coccolithus cribosphaerella* sp. nov., replicated. 4, $\times 14,000$. 5, $\times 12,000$.

Fig. 6. *Maslovella africana* sp. nov., replicated; $\times 17,500$.





boss is observed when the coccolith is found in this position. The distal surface is markedly convex in comparison with the proximal surface.

Size. Longitudinal axis, $3.5-4.2\ \mu$. Transverse axis, $2.7-3.2\ \mu$. Width of shield area, $0.4-0.6\ \mu$.

Remarks. This is a very common and distinctive species and was assigned to the genus *Discolithus* Kamptner 1948 because of its one-shielded nature and the infilled central area.

Discolithus spiralis sp. nov.

Holotype. Plate 70, fig. 3; Plate 71, fig. 4.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1387, depth 320 ft.; Cretaceous.

Diagnosis. Elliptical one-shielded coccolith with the central area infilled with crystals of calcium carbonate arranged in a sigmoid pattern.

Description. Shield composed of approximately 56 overlapping plates. The central area is large and elliptical and completely infilled.

Size. Longitudinal axis, $5.4-5.7\ \mu$. Transverse axis, $3.6-3.7\ \mu$. Width of shield area, $0.3-0.4\ \mu$.

Remarks. This is a very distinctive coccolith and may always be recognized by the sigmoid arrangement of the crystals infilling the central area.

Genus MASLOVELLA Tappan and Loeblich 1966

Synonym. *Covillea* Black 1964.

Maslovella africana sp. nov.

Holotype. Plate 69, fig. 8; Plate 70, fig. 6; Plate 71, figs. 3, 5.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1387, depth 320 ft.; Cretaceous.

Diagnosis. Circular to subcircular asymmetrical coccolith composed of two well-developed shields. At the locality of the axial pore the central area is infilled with crystals of calcium carbonate. The distal shield is larger than the proximal shield and is placed asymmetrically on top of it.

Description. The distal shield is composed of 25-29 overlapping plates, the average number of plates being 25. The plates are wedge-shaped and those situated at the longitudinal polar regions are larger and more markedly wedge-shaped than the remaining plates. The proximal shield is smaller than the distal shield and composed of 25-29 plates of variable size. In the region of the one longitudinal pole are wedge-shaped plates which are only a little smaller than the distal shield plates. At the opposite longitudinal pole all the plates are smaller and less than half the size of the distal shield plates. The central area is infilled with irregularly arranged crystals of calcium carbonate.

Size. Longitudinal axis, $3.1-3.2\ \mu$. Transverse axis, $2.5-2.7\ \mu$. Proximal shield, $1.9-2.6\ \mu \times 2.75-2.9\ \mu$. Distal shield, $3.1-2.5\ \mu \times 4.1-3.7\ \mu$.

Remarks. *Maslovella africana* is common in most of the assemblages studied and characterized by the asymmetrically placed shields. It is tentatively placed in the genus

Maslovella Tappan and Loeblich 1966 which it most closely resembles. Black (1964), however, did not mention in his description of the type specimen any asymmetry in the genus, and thus a new genus might have to be erected. This form has also been found by the author in Type Maestrichtian material sent to him by Dr. E. Martini.

Maslovella blackii sp. nov.

Holotype. Plate 69, figs. 1, 5.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1382, depth 280 ft.; Cretaceous.

Diagnosis. Elliptical two-shielded coccolith. The distal shield is larger than the proximal shield and is composed of 17–27 plates. The central area is completely infilled with crystals of calcium carbonate.

Description. The plates situated at the longitudinal polar region are larger and wedge-shaped while the remaining plates are rectangular in shape and overlap to varying degrees. The structure of the proximal shield is not known but it is thought to be similar to that of the distal shield. The central area is large, elliptical, and completely infilled.

Size. Longitudinal axis, 1.75–2.8 μ . Transverse axis, 1.5–2.0 μ . Width of shield area, 0.5–0.6 μ .

Remarks. During the study of the South African sediments a number of coccoliths were found which were similar to the type description of the genus *Maslovella* (Black) Tappan and Loeblich 1966, except for a few minor differences. Some had only fourteen plates in the distal shield; others had only one well-developed shield and a robust rim in the place of the second shield. The patterning of the central area also varies by having slightly regular to irregular crystals infilling the central area or with two rows of crystals meeting along the longitudinal axis of the ellipse. These forms are thought to be intermediates or broken forms and are all grouped together into *Maslovella blackii*. *Maslovella blackii* differs from *M. africana* in that the latter form possesses a distinct asymmetry of the two shields, whereas the former species is symmetrical.

Maslovella pulchra sp. nov.

Holotype. Plate 69, fig. 3.

Locus typicus. Borehole 'A', Lake Sibaya, Zululand, South Africa. Assemblage 1387, depth 320 ft.; Cretaceous.

Diagnosis. Elliptical coccolith composed of two well-developed shields. The distal shield and the smaller proximal shield are both composed of seventeen plates. The central area is elliptical and infilled with prolongations of the proximal shield plates.

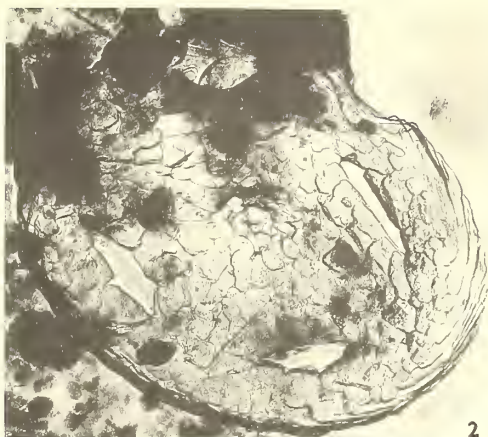
EXPLANATION TO PLATE 71

Figs. 1, 2, 6. *Discolithus rhabdosphericus* sp. nov., replicated. 1, Distal view, $\times 17,500$. 2, Proximal view, $\times 15,000$. 6, Proximal view, $\times 20,000$.

Figs. 3, 5. *Maslovella africana* sp. nov. replicated; 3, Proximal view, $\times 25,000$. 5, Distal view, $\times 16,000$. Fig. 4. *Discolithus spiralis* sp. nov., replicated; Proximal view, $\times 12,000$.



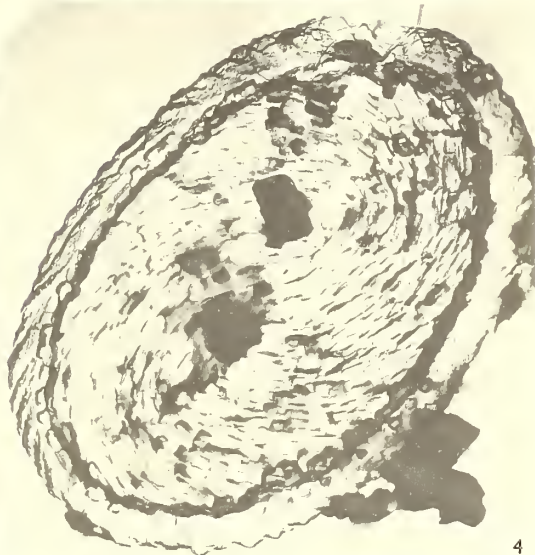
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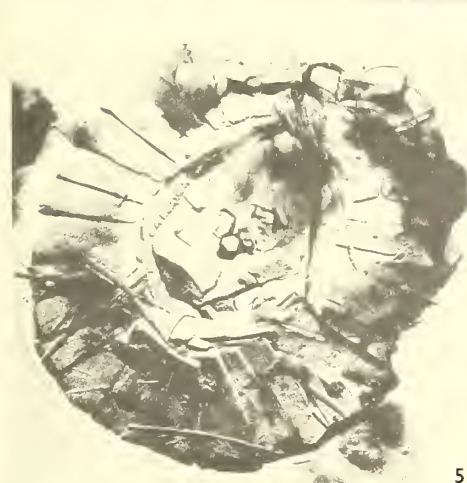
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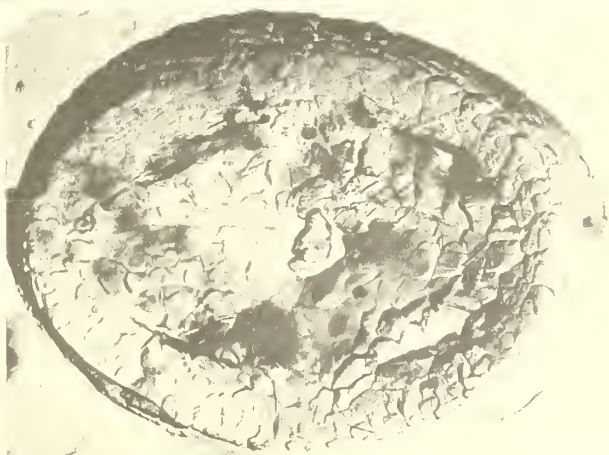
3



4



5



6

Description. The three longitudinal polar plates at each end are larger than the remaining plates and are distinctly wedge-shaped. The proximal shield plates have prolongations which dip inwards towards the central area and meet along the longitudinal axis of the ellipse. The prolongations are rectangular and are on all proximal plates except the six longitudinal polar plates.

Size. Longitudinal axis, 2.0 μ . Transverse axis, 1.4 μ . Width of shield area, 0.5 μ .

Remarks. This form is tentatively placed in the genus *Maslovella* (Black) Tappan and Loeblich 1966 because of the two distinctive shields and the infilled central area. It differs from all the previously described species belonging to this genus in the detail and delicate construction of the central area.

CONCLUSION

The South African material studied is very rich in the remains of these algae and affords excellent opportunity for a more detailed investigation of the coccolith flora of both earlier and later horizons. The work reported in this paper is only a portion of the work done on the Upper Cretaceous of Zululand, South Africa. The remainder of the new species and variations of existing species will be described in later papers.

At present a detailed account of the microstratigraphy of the Cretaceous of Zululand is being prepared. The age of the strata from which the coccoliths were described was determined by the presence of Maestrichtian foraminifera (De Gasparis 1967); this conclusion was supported by the occurrence of Maestrichtian coccoliths.

Acknowledgements. The author is indebted to Anglo-Transvaal Consolidated Investment Company who sponsored this study and provided the material. To Dr. G. F. Hart the author is grateful for his advice and help.

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RICHARD N. PIENAAR
 Department of Plant Biology
 University of Natal
 Durban
 South Africa

A NEW EOCENE CASSIGERINELLA FROM FLORIDA

by W. G. CORDEY

ABSTRACT. A new species of *Cassigerinella* (*C. eocaenica*) is proposed for specimens obtained from an Eocene sample taken off Blake Plateau, Florida. The species is similar, but quite distinct from the Oligocene marker *C. chipolensis* (Cushman and Ponton 1932). Therefore the stratigraphical value of the overlap in ranges of *C. chipolensis* with *Pseudohastigerina micra* (Cole 1927) as indicators of basal Oligocene is not affected.

THE joint occurrence of the species *Pseudohastigerina micra* (Cole 1927) and *Cassigerinella chipolensis* (Cushman and Ponton) has been regarded as a means of recognizing the basal Oligocene, at least within the tropical and semi-tropical belts. This overlap was first recognized by Blow and Banner (*in* Eames *et al.* 1962, p. 68) as a further criterion for the recognition of their zone of *Globigerina sellii* Borsetti 1959 (= *G. oligocaenica* Blow and Banner 1962). Saunders and Cordey (1965) also recognized this overlap in a study of the Oceanic Formation of Barbados. It occurred in samples immediately overlying deposits of definite Eocene age containing such forms as *Hantkenina* spp., *Globorotalia centralis*, and *G. cerro-azulensis*. Bolli (1966), in a general review of world-wide planktonic zonations, added further support to the stratigraphic value of this observed overlap.

Saito and Bé (1963) established an Oligocene age (*sensu* Eames *et al.*, *op. cit.*) for the Vicksburg group of the Gulf Coast region. However, they stated (p. 704) that *C. chipolensis* and *P. micra* occurred together with Eocene forms (e.g. *Hantkenina alabamensis*, *H. primitiva*, *Globorotalia cerro-azulensis*) from a core taken off the Florida coast (Lamont Core A167-21, 29° 49' N., 79° 39' W.). This record therefore cast considerable doubt on the stratigraphic value of this overlap as far as the recognition of the Eocene-Oligocene boundary or basal Oligocene was concerned. Blow examined these cassigerinellids and concluded (*pers. comm.*) that they were different from *C. chipolensis*. Through the kindness of Drs. Bé and Saito the writer obtained material which contained the same form of *Cassigerinella* with *Hantkenina* spp., but from a location to the north of the Lamont Core, at Blake Plateau, 30° 04.8' N., 79° 14.5' W., Sample J.6B.

A careful comparison of the cassigerinellids in the Blake Plateau material with *C. chipolensis* from both the *Globigerina ampliapertura* zone of Trinidad and the Oceanic Formation of Barbados indicates that the Eocene specimens differ from *C. chipolensis*. In view of the stratigraphic significance of *C. chipolensis*, it is desirable that a new species should be erected for these Eocene occurrences.

SYSTEMATIC DESCRIPTIONS

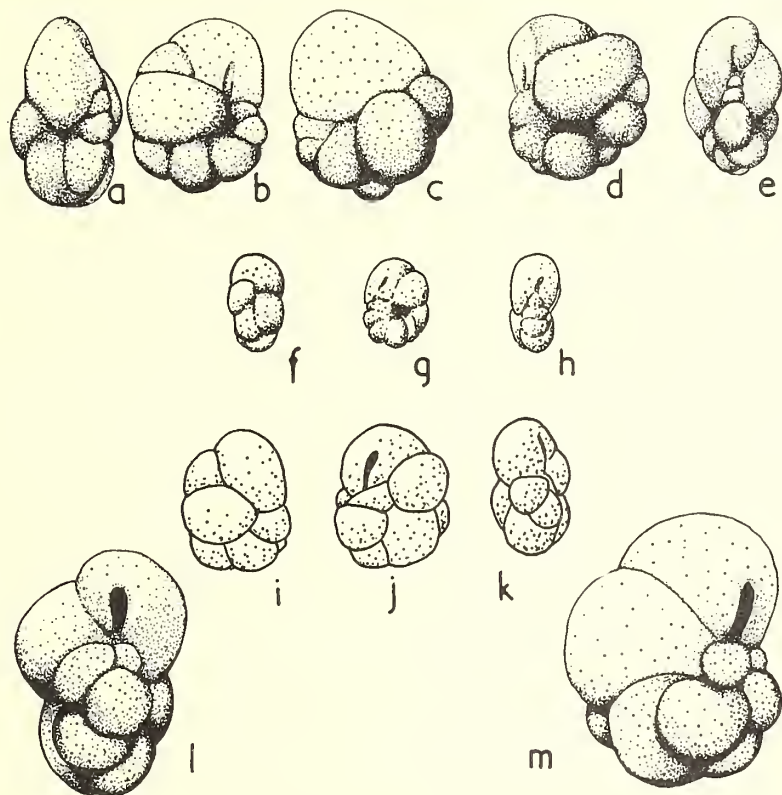
Genus CASSIGERINELLA Pokorný 1955

Cassigerinella eocaenica sp. nov.

Text-fig. 1a-e

Description. Test very small, calcareous, perforate; 8-9 chambers in the final whorl, showing a gradual and uniform increase in size, moderately inflated. Initial two (possibly

three) chambers planispirally arranged, later becoming biserial alternating, but coiled in the same plane. Periphery lobulate, initially sub-acute, becoming sub-rounded, sutures distinct, depressed, curved. Aperture a latero-marginal, extra-umbilical arch.



TEXT-FIG. 1.

a-e, *Cassigerinella eocaenica* sp. nov. Sample J-6b, 30° 04·8' N., 79° 14·5' W., 215' from top. *a-c*, Holotype, BMNH P46838; *d, e*, Paratype, BMNH P46839; both $\times 300$.

f-m, *Cassigerinella chipolensis* (Cushman and Ponton). *f-h*, Dissected hypotype showing penultimate whorl, early chambers planispirally coiled, later chambers alternating; *G. ampliapertura* Zone, Cipero Coast, Trinidad; BMNH P46840, $\times 213$. *i-k*, After Cushman and Ponton, $\times 150$. *l, m*, Hypotype, *G. ampliapertura* zone, Cipero Coast, Trinidad; BMNH P46841, $\times 275$.

Remarks. *C. eocaenica* is similar to *C. chipolensis*, but differs in being consistently smaller, the greatest breadth of the final whorl varying from 0·1 to 0·12 mm., the average being 0·1 mm. Measurement of 45 specimens of *C. chipolensis* shows a variation in the breadth of the final whorl from 0·13 to 0·19 mm., the average being 0·16 mm. Secondly, the chambers in the final whorl are less inflated than in *C. chipolensis*. Specimens of *C. chipolensis* from Barbados (Oceanic Formation), from the Cipero Formation of Trinidad and from the Oligocene of Lindi (Blow and Banner in Eames *et al.* 1962, pl. 15, figs. M-N), show a more rapid increase in the size of the chambers of the final whorl

than in *C. eocaenica*. *C. chipolensis* also has a more rounded periphery throughout. Finally, the chamber arrangement in the final whorl of *C. eocaenica* varies from an initial planispiral arrangement to alternating, whereas the chamber arrangement in *C. chipolensis* is entirely alternating throughout the final whorl. The planispiral arrangement is only developed in the first two or three chambers of the penultimate whorl of *C. chipolensis* (text-fig. 1, *f-h*). The only other species which shows any morphological similarity to *C. eocaenica* is *C. globolocula* Ivanova 1958. Pokorný (*in Eames et al.*) agreed that his species *C. boudecensis* was probably conspecific with *chipolensis*, and considered that *globolocula* was 'certainly conspecific with *boudecensis*' (*op. cit.*, p. 83). The writer would agree with this conclusion and therefore the above remarks on *C. chipolensis* and *C. eocaenica* apply equally to *C. globolocula* (and also *C. boudecensis*).

Deposition of types. Holotype and paratype specimens are deposited in the British Museum (Natural History). An unfigured paratype is deposited in the United States National Museum, No. 643514.

Material. Fifteen specimens of *C. eocaenica*; forty-five specimens of *C. chipolensis*.

Acknowledgements. The author is grateful to Drs. Bé and Saito (Lamont Geological Observatory, Columbia University, New York) for the donation of the samples upon which this study is based; Dr. R. Lagaaij and J. A. Postuma (Bataafse Internationale Petroleum Maatschappij N.V., The Hague), for their critical reading of the manuscript; and the Bataafse Internationale Petroleum Maatschappij N.V., for permission to publish this paper.

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W. G. CORDEY
Bataafse Int. Petr. Mij.
EP/12, Carel van Bylandtlaan 30
The Hague
Netherlands

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MORPHOLOGY AND PHYLOGENY OF *ORBULINOIDES BECKMANNII* (SAITO 1962)

by W. G. CORDEY

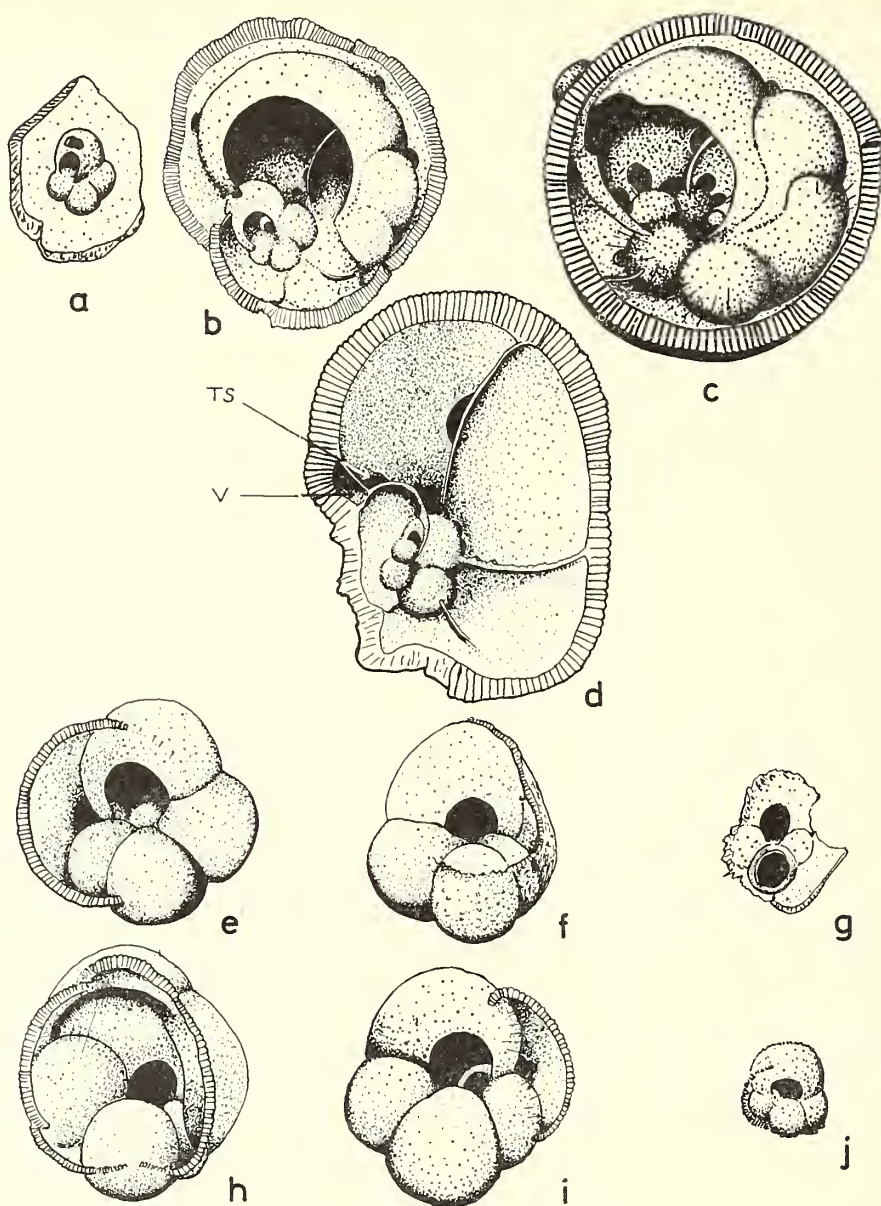
ABSTRACT. An examination of dissected specimens of the Eocene species *Orbulinoides beckmannii* (Saito 1962), formerly *Porticulasphaera mexicana* (Cushman 1925), reveals certain morphological features not hitherto described. A study of the ontogeny of *O. beckmannii* and a comparison with the contemporaneous species *Globigerapsis kugleri* Bolli, Loeblich and Tappan, and *Globigerinatheka barri* Bolli, Loeblich and Tappan, indicate that *O. beckmannii* is unlikely to be related to either of these species. It appears to have developed from some globorotaloid ancestor.

THIS study is based on specimens obtained from a block of extraneous Eocene in the Miocene Nariva Formation of Trinidad. This same material was used by Bolli (1957*b*, p. 159) in his monograph on the Eocene faunas of Trinidad. Bolli, Loeblich and Tappan (1957, p. 34) gave a full and accurate description of their new genus *Porticulasphaera*, and Bolli (1957*a*, p. 116) in placing the Miocene species *Globigerinoides glomerosa* Blow 1965 in this new Eocene genus commented that detailed comparative studies would probably '... reveal differences between the Eocene and Miocene forms ...' (op. cit., p. 115). Bolli, Loeblich and Tappan designated *Globigerina mexicana* Cushman 1925 as the type species of their new genus *Porticulasphaera*. Saito (1962) considered that the Cushman type should be referred to the genus *Globigerapsis* Bolli, Loeblich and Tappan. Further examination of *G. mexicana* by Saito, and independently by Blow, has led to the conclusion that *G. mexicana* Cushman is conspecific with *Globigerapsis semiinvoluta* (Keijzer 1945). The writer has also examined the holotype of *G. mexicana* and agrees with their conclusion. Blow and Saito have therefore assigned the specimens which Bolli (1957*a*) previously referred to as *Porticulasphaera mexicana* (Cushman 1925), and upon which this study is based, to the new genus *Orbulinoides* as *O. beckmannii* (Saito 1962).

Olsson (1965) subsequently erected the genus *Praeorbulina* for the Miocene forms (i.e. *Porticulasphaera* of Bolli 1957*a*, p. 115) with the type species *Globigerinoides glomerosa glomerosa* Blow 1956. The object of this paper is to discuss certain morphological features observed in *O. beckmannii*, and which have not previously been described.

Morphology. Externally *O. beckmannii* shows numerous apertures at the base of the final chamber. The early trochospiral part of the test shows between one and four supplementary apertures; occasionally no such apertures were present. When present they are usually located at the junction of the spiral and intercameral sutures. The specimen illustrated by Bolli (1957*a*, pl. 37, fig. 1*a*) showing eight such apertures is considered atypical (cf. Bolli, Loeblich and Tappan, 1957, pl. 6, figs. 9*a*, *b*).

A removal of the final chamber and part of the walls of the last three chambers of the initial trochospire (text-fig. 1*c*) reveals the numerous supplementary apertures described by Bolli, Loeblich and Tappan (1957) and Olsson (1965). However, a closer examination



TEXT-FIG. 1. *a-d*, *Orbulinoides beckmannii* (Saito 1962). *a*, Dissected specimen showing earliest whorl with an umbilical-extra-umbilical aperture, BMNH P46842, $\times 76$. *b*, *c*, Dissected specimens, BMNH P46843, 46844, $\times 105$. *d*, Dissected specimen showing trochospiral supplementary aperture (TS) opening into the vestibule (V), BMNH P46846, $\times 93$.

e-g, *Globigerinopsis kugleri* Bolli, Loeblich and Tappan 1957. Dissected specimens showing globigerinid primary aperture; *e*, Specimen with Bulla partly removed, $\times 120$; *f*, Bulla and two chambers removed, $\times 120$; *g*, Bulla and five chambers removed; BMNH P46847, $\times 105$.

h-j, *Globigerinatheka barri* Bolli, Loeblich and Tappan 1957. Dissected specimens showing a globigerinid primary aperture; *h*, Bulla partly removed, $\times 100$; *i*, Bulla and two chambers removed, $\times 100$; *j*, Bulla and five chambers removed; BMNH P46848, $\times 73$.

All specimens from the *O. beckmannii* Zone, Navet Formation, Eocene, Point-à-Pierre, Trinidad.

of these apertures shows that in no instance are they directly connected with the outside of the test. They open into a small cavity (here termed vestibule) between the thick outer wall and the delicate wall of the initial trochospirally arranged chambers (text-fig. 1e). This vestibule is usually situated at the junction of the spiral and intercameral sutures, but probably also extends some way along the intercameral suture. It is also seen that the external supplementary apertures on the initial trochospire were never aligned with the internal apertures. Therefore, there is only an *indirect* connexion, that is via the vestibule, between the inside and outside of the test, as far as the early supplementary apertures are concerned.

Bolli's comparison (op. cit., p. 115) of the supplementary apertures of *Orbulinoides* and *Globigerinoides* cannot be upheld. There is a basic difference in that, in the latter genus, these apertures are never covered by subsequent thickening of the test and are in direct communication with the inside of the test. It would seem that early supplementary apertures became vestigial structures, in the sense that the degree of direct connexion between the inside and outside of the test in this area was much reduced. This appears to be in contrast with species of *Globigerinoides* (and also *Orbulina suturalis* Bronnimann 1951) where a direct connexion is maintained for each of the apertures.

The method of test thickening in *Orbulinoides* also appears to be in contrast with certain fossil species of *Globigerinoides* (e.g. *G. subquadratus* Bronnimann 1954 = *G. ruber* (d'Orbigny 1826) of Bolli 1957a). In this genus thickening is progressive rather than occurring only after the adult stage has been reached.

A consideration of the morphology of the initial trochospire of *Orbulinoides* (e.g. its large primary aperture, inflated spinose chambers, numerous large supplementary apertures, and thin wall) strongly suggests that during the trochospiral stage the animal inhabited the epipelagic zone (*sensu* Hedgepeth 1957, p. 18, fig. 1). The subsequent test thickening, and the reduction in the number of supplementary apertures, might be correlated with its migration to deeper levels. The work of Bé and Ericson (1963) and Bé (1965) offers some support for this view, since a correlation between the thickness of the test with depth in the Recent species *Globorotalia truncatulinoides* and *Globigerinoides sacculifera* (Brady) was observed. The reduction in the number of 'functional' supplementary apertures may have been one means of increasing its weight in order to occupy lower levels. It is equally possible that the thickening of the test and reduction in supplementary apertures are associated with reproduction. The final inflated chamber may represent a type of brood pouch.

The presence of such an inflated final chamber in *Globigerapsis* and *Globigerinatheka* may indicate a similar mode of reproduction in these genera. Le Calvez (1936) showed that in *Orbulina minima* (d'Orbigny) there was a gradual reduction in the globigerine part of the test with depth. Furthermore, in specimens from the deepest levels (about 300 m.) the globigerine chambers had completely disappeared, and all that remained was the spheroidal final chamber which was frequently found to be filled with gametes. Therefore, there is some support for the view that the inflated final chambers of these Eocene genera might be connected with reproduction.

Phylogeny. Bolli (1957a, p. 160) stated that '. . . *Globigerapsis*, *Globigerinatheka* and *Porticulasphaera* obviously represent a related group'. He considered that *Globigerapsis index* (Finlay) gave rise to *G. kugleri* Bolli, Loeblich and Tappan, from which *O.*

beckmannii developed. His further support for this view was the fact that the three genera showed a 90 per cent. tendency to coil dextrally. Bolli is correct in the case of *Globigerapsis* and *Globigerinatheka*, and Eckert's (1963) study of these genera supports this conclusion. However, in the writer's opinion, *Orbulinoides* is unrelated to either of these genera. The gross morphological similarity of these three species is more likely to be a function of convergent evolution than any genetic affinity (at least as far as *beckmannii* is concerned). This view is based on a comparison of the ontogeny of *G. kugleri*, *G. barri*, and *O. beckmannii* (text-fig. 1). It is clear that both *kugleri* and *barri* have arisen from a globigerinid ancestral form, while *O. beckmannii* shows an unmistakable umbilical-extra-umbilical primary aperture initially, and therefore is derived from a globorotaloid ancestor. The striking differences in the morphology of the initial whorls, particularly the distinctive shape of the later trochospiral chambers of *beckmannii*, and the large primary aperture, adds further support to this view (text-fig. 1, cf. figs. *a*, *b* with *f-j*). Bolli considered the gross similarity of the adult tests of these three species the most important phylogenetic factors. The writer, however, considers that the evidence of the ontogeny of these species outweighs the adult similarity in gross morphology.

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W. G. CORDEY

Bataafse Int. Petr. Mij.

EP/12, Carel van Bylandtlaan 30

The Hague

Netherlands

Typescript received from author 29 June 1967

THE GASTRIC CONTENTS OF AN ICHTHYOSAUR FROM THE LOWER LIAS OF LYME REGIS, DORSET

by JOHN E. POLLARD

ABSTRACT. The partial skeleton of a small ichthyosaur associated with the gastric mass is described from the Lower Lias of Lyme Regis. The gastric mass was oval in shape and composed of minute dibranchiate cephalopod hooklets in random orientation. Four distinct types of hooklet are recognized in these gastric contents.

Examination of published records and museum specimens suggests that gastric contents composed of cephalopod remains are more commonly preserved than those of fish remains. A study of ichthyosaur coprolites shows a predominance of defecated fish remains and an absence of hooklets from these structures. The diet, mode of feeding, and digestive mechanism of Liassic ichthyosaurs, in comparison with a teuthophagous cetacean, the sperm whale, are considered.

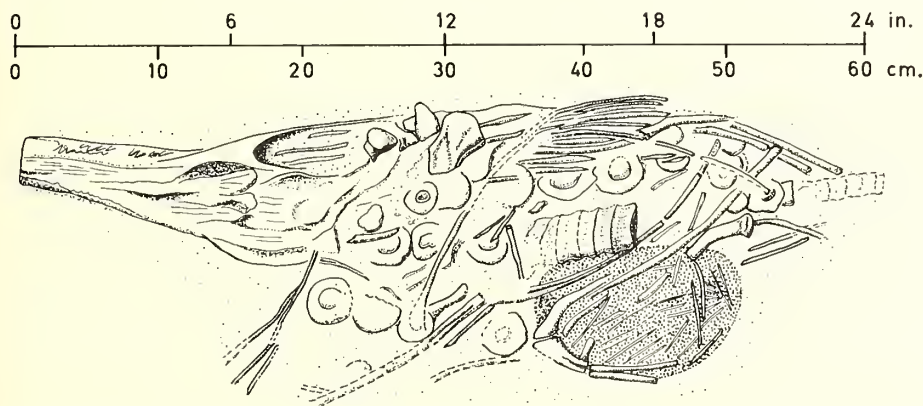
IN April 1963 the skeleton of a small ichthyosaur was found in the shales of the Lower Lias on the foreshore west of Lyme Regis, Dorset. Unfortunately due to the exposed location of this specimen, in soft shaly-mudstone at about the half-tide level, only a short time was available for its extraction. Only the anterior part of the skeleton could be recovered consisting of parts of the skull, pectoral girdle, vertebral column, and ribs. Careful preparation of this material showed that the skeleton was crushed and slightly dismembered, but that the stomach contents were preserved as a dark discrete area underneath the vertebral column and ribs. Such occurrences are fairly well known, but the good state of preservation and lack of dispersal of the stomach contents of this specimen make them worthy of detailed description, quantitative analysis, and discussion in terms of the feeding habits and digestive mechanism of the Liassic ichthyosaurs.

DESCRIPTION

Horizon and locality. The specimen was collected from the shales of the lower part of the *Psiloceras planorbis* Zone of the Lower Lias (Woodward and Ussher 1911, p. 38), at the south-east corner of Pinhay Bay, two miles west of Lyme Regis (National Grid Reference: SY 325907). The enclosing sediment was a poorly fossiliferous silty and shaly mudstone, which was interbedded with thin limestones and shales containing *Liostrea liassica*, *Hemicidaris* spines, and rarely *Plagiostoma gigantea* and *Psiloceras planorbis*. No other vertebrate remains or coprolites were observed at this horizon.

Skeletal remains. The partial skeleton of the ichthyosaur extracted was 2 ft. (60 cm.) in length and consisted of the skull and parts of the vertebral column, pectoral and pelvic girdles, rib cage, and a paddle. (The specimen is now preserved in the collections of the Geology Department, University of Manchester, registration number SF.1.) Text-fig. 1 is drawn from a field photograph of the specimen *in situ*, and shows the relative positions of the bones and the gastric mass from the dorsal aspect. The prepared skeleton can be examined both dorsally and ventrally, Plate 72, figs. 1 and 2, and enables the individual bones to be identified.

The skull is 10 in. (25 cm.) long, crushed dorso-ventrally and twisted sinistrally. The anterior part of the snout is missing, but the premaxilla and eleven upper jaw teeth and thirteen lower jaw teeth on the right side of the mouth are visible on the upper surface (Pl. 72, fig. 1). On the under surface of the skull both dentary bones are present and twenty-three upper jaw teeth, and sixteen lower jaw teeth, from the left side of the mouth (Pl. 72, fig. 2). The teeth appear to be well formed typical ichthyosaur teeth, up to 13 mm. in length exposed, with smooth apices and bifurcating grooves on the crown. The form of the tooth crown is close to that of *Ichthyosaurus communis* Conybeare as figured by Owen (1881, pl. 24, fig. 5). The anterior part of the right orbit was present dorsally



TEXT-FIG. 1. Ichthyosaur skeleton *in situ* in the Lower Lias west of Lyme Regis, showing the relationship of the various bones to the gastric mass. Widely spaced fine stippling represents the shale matrix, while the closely spaced coarser stippling represents the gastric contents.

(text-fig. 1) but no sclerotic plates were seen. The hind part of the skull is badly crushed, and the only other bones clearly recognizable are displaced fragments of the articular and basioccipital (Pl. 72, fig. 1).

The post-cranial skeleton is represented by a total of twenty-eight vertebrae and numerous fragments of single and double ribs. On the upper (dorsal) surface of the specimen, Pl. 72, fig. 1, seven thoracic vertebrae occur in a row from 4 to 8 in. (10–12 cm.) behind the skull, and bound the gastric mass dextrally. The dorsal left boundary of the gastric mass is formed by a series of parallel double ribs (text-fig. 1 and Pl. 72, fig. 1), while a complex of complete and broken double and single ribs are elsewhere compressed into the gastric mass dorsally.

The anterior boundary of the gastric mass on the ventral side of the specimen is formed by the bones of the pectoral girdle (Pl. 72, fig. 2). Parts of the left coracoid, humerus, and scapula are clearly recognizable and are impressed into the gastric mass ventrally. The interclavicle is present, and fragments of fifteen phalangeal bones of the left anterior paddle were found just beyond the humerus. The only other recognizable bones collected were a displaced pubis and three phalangeal bones of a posterior paddle, Plate 72, fig. 1, all occurring postero-dextrally of the gastric mass.

The nature and arrangement of these skeletal remains suggest that there had been a fair amount of displacement of the bones during burial and that the gastric mass must

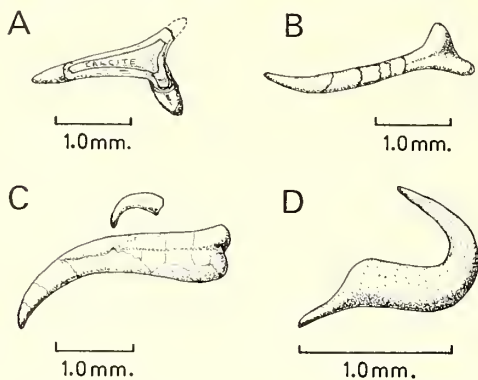
have been trapped in an unusually anterior position, crushed between the anterior-dorsal thoracic rib cage and the pectoral girdle.

Gastric mass. The gastric mass of this specimen, text-fig. 1, was broadly oval in shape, compressed dorso-ventrally, 13.5 cm. long from anterior to posterior, and 8.5–9.0 cm. wide from right to left of the skeleton. Only the anterior part of the mass (8 cm. anterior to posterior by 7 cm. right to left) was collected and prepared for further study (Pl. 72, fig. 1; Pl. 73, fig. 1). Estimates of the dorsal area of the stomach mass, measured from the field photograph vary from 85.5 to 95.5 sq. cm. or approximately 90 ± 5 sq. cm. The depth or thickness of the dorso-ventral cross section of the gastric mass was measured accurately on the prepared specimen (Pl. 73, fig. 1), using a travelling microscope, and varied from 0.25 to 0.75 cm., with a mean value of about 0.33 cm.

The cleaned and prepared dorsal and ventral surfaces of the gastric mass, Plate 72, fig. 2; Plate 73, figs. 1 and 2, show that the stomach contents preserved consist of a densely packed mass of dibranchiate cephalopod hooklets and rare large quartz grains. These hooklets are packed in random orientation (Pl. 73, fig. 2) in a matrix of finely crystalline calcite. The quartz grains are sub-angular or sub-rounded in shape from 0.25 to 1.40 mm. in diameter, sparsely distributed

on the dorsal surface, but occurring in considerable concentration in patches of the ventral surface of the mass (i.e. at point X on Pl. 72, fig. 2).

Three, or possibly four, distinctly shaped types of hooklet can be recognized in these contents, types A, B, C, and D of text-fig. 2. Type A is relatively short straight spinose form with a strongly bifid base, rather like an odontaspide shark's tooth in shape. Type B is longer and more slender than type A, with a less pronounced base and a gentle curve along its length. Type C is broader bladed than types A and B, has distinct lateral flattening, and a strong, nearly 90°, hook. The base of type C is much less pronounced than on types A or B, but this character may be suppressed due to lateral flattening. Type D of text-fig. 2 is extremely rare in the gastric contents, about 1 mm. or less in size, and a specimen from a different horizon and locality is figured here for comparative purposes, the significance of which will be discussed later. Each of these hooklet types

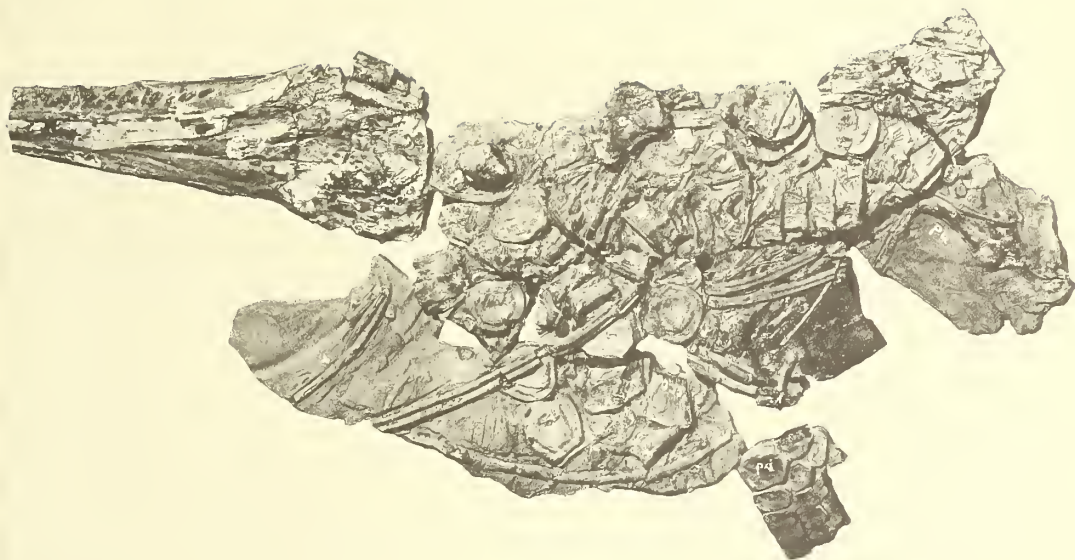


TEXT-FIG. 2. Cephalopod hooklets from the Lias. Types A, B, and C are all drawn from hooklets in the gastric contents shown on Plate 73, figs. 1 and 2, while type D is drawn from specimen OUM. J.14800, in mudstone from the Upper Lias at Dumbleton, Gloucestershire.

EXPLANATION OF PLATE 72

Fig. 1. Dorsal view of prepared ichthyosaur skeleton preserved with gastric contents. Lower Lias, Planorbis Zone, Lyme Regis, Dorset. SF.1. Geology Dept. Collections, University of Manchester. *a.*, articular; *v.*, vertebra; *r.*, rib; *sca.*, scapula; *pd.*, paddle; *pub.*, pubis.

Fig. 2. Ventral view of ichthyosaur specimen SF.1. Symbol 'X' indicates the region of the ventral surface of the gastric mass with a concentration of quartz grains. *d.*, dentary; *sa*, supra-articular; *icl.*, interclavicle; *cor.*, coracoid; *hum.*, humerus.



1



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POLLARD, Ichthyosaur gastric contents



in the gastric contents shows considerable size range, for instance in terms of length, type A varies from 1.0 to 1.90 mm. (10 measured), type B from 0.70 to 3.00 mm. (16 measured), and type C from 0.9 to 2.90 mm. (22 measured). Types B and C appear to be commoner than type A in the mass.

All these hooklets seem to be composed of a jet black and very brittle organic, possibly chitinous, material. They are all hollow although sometimes filled with crystalline calcite. Due to their brittle nature and hollow centre, most of the hooklets are cracked and partially crushed and splinter if any attempt is made to separate them from the mass.

In an attempt to determine the approximate number of hooklets on the dorsal surface of the gastric mass, the distribution of the hooklets in an area 2 cm. square was plotted from the enlarged photograph, Plate 73, fig. 2. The frequency of hooklets on this surface varied between 450 and 540 per sq. cm., with a mean of about 500 per sq. cm. This number represents only those hooklets that could be clearly identified and is, therefore, a minimal estimate. The total number of hooklets on the dorsal surface of the gastric mass, area 90 ± 5 sq. cm., is about $45,000 \pm 7,000$ (i.e. $90 \pm 5 \times 500 \pm 50$).

It has proved very difficult to estimate the total number of hooklets in the gastric mass due to their being crushed and randomly orientated. The cross-sectional diameter of a number of hooklets of various sizes, uncrushed on the dorsal surface, varied from 0.20 to 0.50 mm. The mean depth of the gastric mass is 0.33 cm., so that allowing for parallel packing and no crushing, the hooklets would be from approximately $16 (3.30/0.2)$ to $7 (3.30/0.5)$ layers deep. Making an allowance for crushing and random packing, from 6 to 14 or 10 ± 4 layers deep, would seem to be a reasonable estimate. Therefore, the total number of hooklets in the gastric mass is $45,000 \pm 7,000 \times 10 \pm 4 = 478,000 \pm 250,000$ or $478,000 \pm 53$ per cent. Such a large error is unavoidable in such approximate calculations, but the figure gives some idea of the correct order of magnitude.

DISCUSSION

In order to understand the significance of the gastric contents previously described, and the precise nature of the dibranchiate remains they contain, a search has been made in the literature and other specimens have been examined in several British museums. The author does not intend this as an exhaustive treatment of the subject, but more as a spur to examination and comment by other workers.

Other Liassic ichthyosaurs with gastric contents. Ichthyosaur remains with associated gastric contents preserved have been known for more than a hundred years from the Liassic shales of Lyme Regis and Whitby in England, and Holzmaden in Germany. Buckland in the *Bridgewater Treatise* (1836) is among the earliest English records. He described and figured (pl. 13 and 14) two ichthyosaur specimens from Lyme Regis that contained a coprolite mass with fish scales, preserved within the abdominal cavity. These specimens are in the collections of the Oxford University Museum and will be discussed later in this paper.

Probably the earliest description of the preserved cephalopod hooklets associated with ichthyosaur bones is that of Coles (1853). He describes a layer of carbonaceous material made up of 'minute black points'—hollow and filled with calcite, that was found

adhering to an ichthyosaur vertebra from the Lias of the Tewkesbury district. His excellent figures (pl. 5, figs. 2 and 13) show shape, size, and crack patterns identical to the hooklets described and figured in this paper (Pl. 73, fig. 2 and text-fig. 2). This material was wrongly identified by Coles (1853, p. 81) as 'setiform or bristly scales' of the ichthyosaur integument, and was reported by him to be known associated with ichthyosaur skeletons from the Lias of Lyme Regis and Ilminster as well as Tewkesbury. Cole's error was corrected by Moore (1856), who reported finding stomach contents composed of cephalopod arm hooklets in sixteen out of twenty-three Liassic ichthyosaur skeletons he had prepared for his museum. Moore examined the gastric contents further, and suggested that they consisted of the desiccated ink and arm hooklets of naked Jurassic cuttle-fish allied to *Onychoteuthis*.

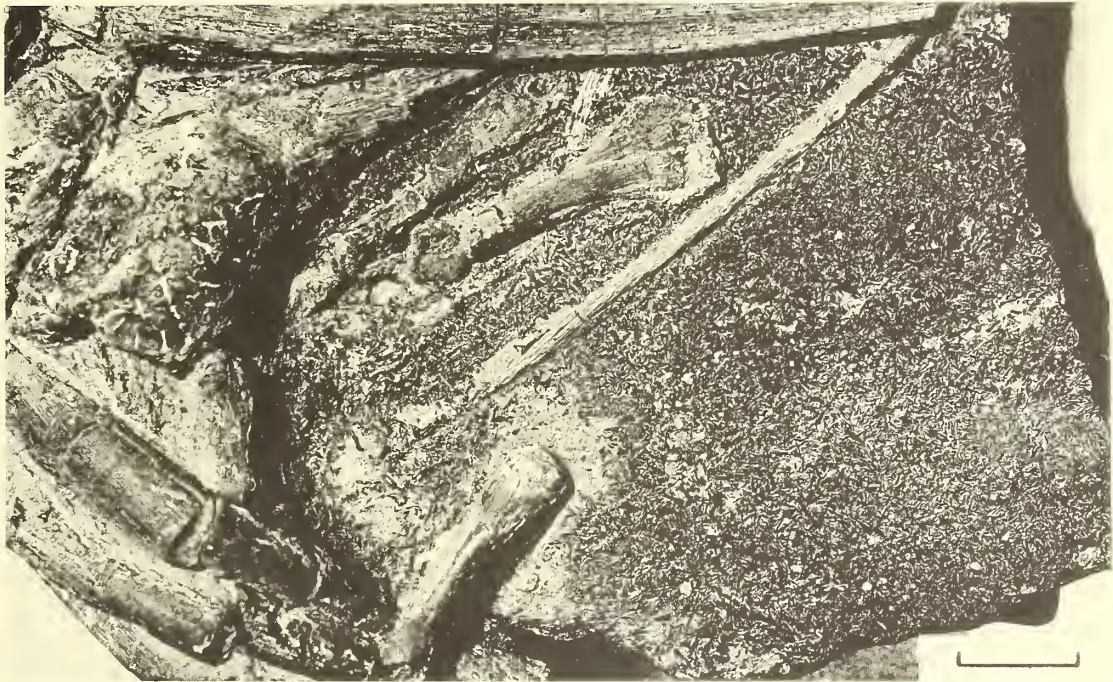
Buckman (1879), when describing a new species of fossil dibranchiate *Belemnoteuthis montefiorei* from the Lower Lias of Charmouth, mentions the frequent occurrence of ichthyosaur stomach contents and coprolites full of cephalopod arm hooklets. Similar general statements recording gastric contents composed largely of cephalopod hooklets have been made by several workers studying ichthyosaurs from the Holzmaden Lias (Seeley 1880, Branca 1908, Drevermann 1914, Huene 1922, Hofmann 1958, and Augusta 1964). Wurstemberger (1876) described a Holzmaden specimen of *Stenopterygius quadriscissus*, with head 50 cm. long, vertebral column 240 cm. long, where a large stomach mass of fish and cephalopod remains was found only 20 cm. behind the head. This unusually anterior thoracic position of the stomach is very similar to that of the specimen described here. Williston (1914, p. 123) refers to an ichthyosaur skeleton in the Stuttgart Museum that has preserved in its stomach contents the remains of more than 200 belemnites. Dr. K. D. Adam (pers. comm.) informs me that no such specimen exists in the Stuttgart Museum, but Williston's comment is probably a mistaken reference to a well preserved specimen of the shark *Hybodus* from the Upper Lias of Holzmaden described by Brown (1900) and later Shimanskiy (1949). The gastric contents of this shark contain over 250 belemnite rostra.

Many British museums possess in their collections ichthyosaur skeletons with well preserved gastric contents. On other specimens the gastric contents have obviously been cleaned off in the preparation of the skeleton, and so it would appear that these contents are of much commoner occurrence than the literature would suggest. The ichthyosaurs figured by Buckland (1836, pls. 13 and 14) are preserved in the Oxford University Museum, numbered specimens J.13587 and J.13593 respectively. Re-examination of these specimens by the author confirms that Buckland's figures and descriptions are extremely accurate and that the gastric contents consist largely of scales and spines of the Liassic fish *Pholidophorus* sp., set in a matrix of a pale buff coprolitic clay. The larger specimen J.13593 (Buckland 1836, pl. 14) does have a very sparse scattering of type C hooklets over the whole dorsal surface of the gastric mass. Three other specimens

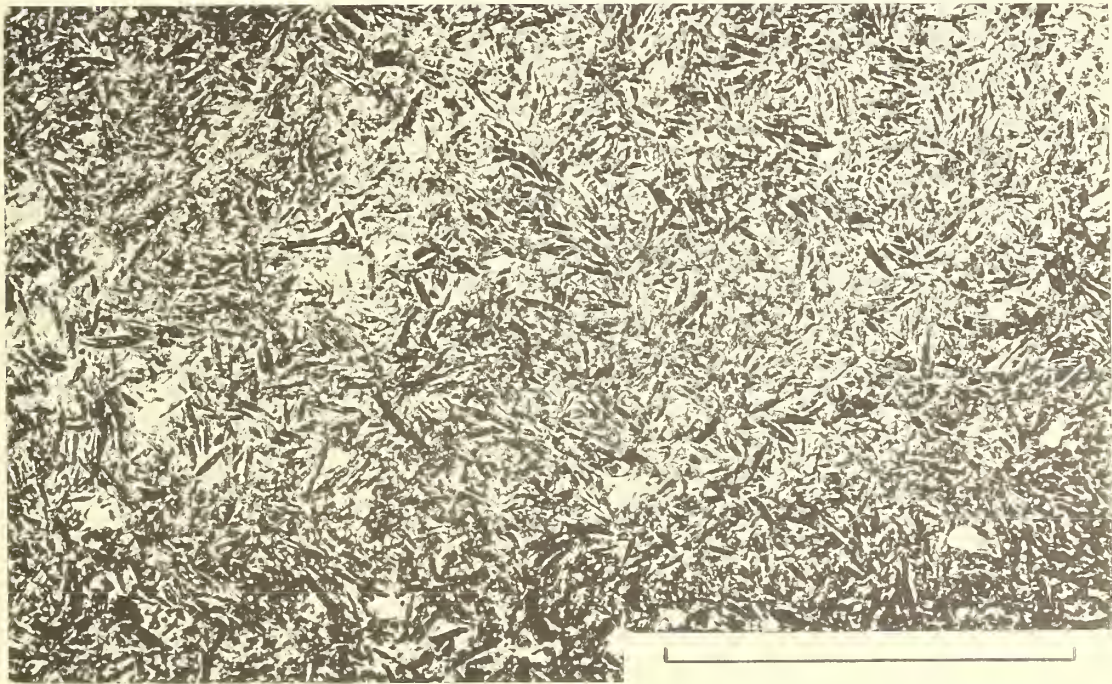
EXPLANATION OF PLATE 73

Fig. 1. Dorsal view of the gastric mass and associated bones of ichthyosaur specimen SF. 1 (compare with Pl. 72, fig. 1). Scale of 1 cm.

Fig. 2. Magnified view of part of the dorsal surface of the gastric mass of specimen SF. 1 showing the various types of cephalopod hooklets present. (This field of view may be orientated on Pl. 73, fig. 1, by the arcuate row of five large quartz grains in the lower half of the picture.) Scale of 1 cm.



1



2



of Liassic ichthyosaurs from Lyme Regis in Oxford University Museum, J.12125, J.13592, and J.10348, all contain patches of gastric material, composed of types A, B, and C hooklets, in the thoracic or anterior abdominal regions. The gastric mass in each case is identical to the specimen described here, just hooklets without any matrix of the coprolitic clay seen in Buckland's specimens.

Specimens of various species of ichthyosaur from the Lower Lias at Lyme Regis on display in the public galleries of the British Museum (Natural History) show gastric contents of densely packed hooklets devoid of matrix (e.g. BMNH 36256, BMNH R1614, BMNH R1072, BMNH 38523, BMNH 43006, and BMNH R1896). In the Manchester Museum an excellent specimen from the Upper Lias at Whitby has a large gastric mass containing A, B, and C type hooklets, just posterior to the pectoral girdle.

The conclusion to be derived from a study of these listed, and other specimens, is that gastric contents of densely packed dibranchiate cephalopod hooklets are much commoner in prepared specimens than the fish remains in a matrix of coprolite clay described by Buckland. The gastric contents of many Jurassic plesiosaurs are also known to be composed largely of dibranchiate hooklets (Juravlev 1943, Hekker and Hekker 1955, and Tarlo 1959), but here large gastroliths usually occur as well (Seeley 1877, Brown 1904, and Williston 1904). Gastroliths have not been found preserved in ichthyosaur stomach contents.

Contents of coprolites from Lower Lias. Well-preserved coprolites, usually assigned to ichthyosaurs or plesiosaurs, have been known from the Lower Lias at Lyme Regis since before Buckland's classic paper of 1835. Most of these coprolites are assumed to have been formed by ichthyosaurs, on account of their similarity in composition to material described by Buckland (1836) from within the ichthyosaur abdominal cavity. Other workers (Fraas 1891 and Woodward 1917) have questioned the assignment of these coprolites to ichthyosaurs. They argue that spirally folded coprolites are rarely found associated with ichthyosaur skeletons and are more likely to have been formed by the spiral intestine of Liassic sharks than by the typical reptilian intestines which the ichthyosaurs probably possessed. The following analysis shows that the majority of Liassic coprolites do not have well-formed spiral folds but have faunal, lithological and chemical features identical to the ichthyosaur gastric contents described by Buckland. Moreover, the hybodont sharks, suggested by Woodward (1917) as probable producers of the coprolites, are believed on account of their dentition (Romer 1966, p. 40) to have been benthonic or necto-benthonic scavenger feeders, and not nectonic fish feeders as were the producers of the Liassic coprolites.

Buckland (1835) showed that Lower Lias coprolites contain fish remains, bones of young ichthyosaurs, and possibly the sucker rings of fossil cuttle-fish. He did not observe or describe any dibranchiate hooklets. The matrix of these coprolites, which I have called 'buff coprolitic clay', was shown by Buckland to be phosphatic material derived from the digestion of fish and reptile bones. Buckland suggested that the strong spiral involutions frequently seen on coprolites indicate that the small intestine of the ichthyosaur was ribbon like and twisted into a spiral. Firtion (1938) analysed the contents of coprolites from the Lower Lias of Alsace. He found that the undigested contents were mainly crinoids, gastropods, or pelecypods with less abundant foraminifera, ostracods, fish remains, and brachiopod shells. These coprolites rarely had spiral folds and were

obviously formed by a benthonic feeding animal. However, he assigned them to ichthyosaurs, although stomach contents of the above composition are unknown in ichthyosaurs. Such coprolites could as easily belong to teleosaurs or plesiosaurs (Drevermann 1914). Ager (1963, p. 120) mentions that a study of coprolites suggests that Mesozoic ichthyosaurs included belemnites in their diet, but he does not refer to any actual records of this fact.

Fifty well-preserved coprolites from Buckland's collection in the Oxford University Museum have been examined by the author. These specimens vary from 1 to 6 in. in length, mainly 2–3 in. long, and their contents can be examined on the cleaned surface, or internally where they have been sectioned and polished. Forty-five specimens contain recognizable fish remains, mainly scales, fin rays, and spines of *Pholidophorus* sp., less commonly remains of *Dapedium* sp. and *Lepidotus* sp. Two specimens, those figured by Buckland (1835, pl. 29, figs. 2, 3, 4, and 5), contain reptilian bones and fifteen specimens have well-formed spiral involutions. None of these coprolites contain visible remains of dibranchiate hooklets and the possible sucker rings figured by Buckland (1835, pl. 30, figs. 1, 2, and 3) are considered to be transverse sections of fin rays and small vertebrae of fish. Examination of sixteen well-preserved coprolites in Manchester Museum and Geology Department, University of Manchester, shows that all these contain fish scales and spines, none contain reptilian bones, and only four specimens have well-formed spiral folds. One of the Manchester Museum specimens has a small patch of shale matrix with type B and C hooklets adhering to its surface, but they are not contained in the adjacent coprolite material. Lydekker (1889, pp. 114–17) lists sixty-six coprolites from the Lower Lias in the British Museum collections, but only mentions fifteen containing fish scales, only two with reptilian bones, and only one showing well-formed vascular impressions.

From this survey it is suggested that ichthyosaurs from the British Lower Lias primarily defecated fish remains in their coprolites. Undigested cephalopod remains have not been seen in these coprolites, so it may be inferred that they accumulated in the stomach, as their predominance in gastric contents would suggest. The commonest form of fish eaten, *Pholidophorus*, is presumed to have been a nectonic or necto-benthonic form, not a deep bodied benthonic fish like *Dapedium* or *Lepidotus*. The possible significance of this latter observation will be discussed later.

Nature of the cephalopod remains. Throughout the preceding part of this paper the hooklets found in the gastric contents of the ichthyosaur have been broadly described as belonging to Liassic dibranchiate cephalopods. It is of some importance to establish the precise nature of the dibranchiates possessing these hooklets before discussing their relationship to their ichthyosaur predators.

As well as occurring in gastric contents of ichthyosaurs, these hooklets are known preserved in their life position on the arms of predominantly soft bodied dibranchiates that are rarely found in Liassic and other Jurassic argillaceous sediments. Pearce (1842) named one of these soft-bodied dibranchiates with arm hooklets from the Oxford Clay as *Belemnoteuthis*. The arm hooklets of *Belemnoteuthis* were figured by Owen (1844, pl. 6, fig. 2) and Mantell (1852, fig. 4) as all possessing elongated pointed bases, and one form similar in shape to type D of text-fig. 2.

It has already been mentioned that Coles (1853) seems to have been the first person

to describe the hooklets from the Lias, although he was in error about their nature. The suggestion of Moore (1856), that these hooklets belonged to naked dibranchiates allied to *Onychoteuthis*, does not seem to be supported by any earlier published records of specimens of this genus from the Liassic rocks of Britain. Huxley (1864) was the first person to unquestionably associate these forms with belemnoid arm hooklets. He figured (1864, pl. 1, fig. 5a) forms identical with the types A, B, and C of text-fig. 2 when he described two specimens of belemnites from the Lias (BMNH 74106 and BMNH 39855), where soft parts were preserved in association with the guard, phragmocone, and proostracum. One of these specimens, BMNH 74106, must be interpreted with some caution as it has been restored in preparation. Dr. K. A. Joysey (pers. comm.) has informed me that one such specimen (J42835) in the Sedgwick Museum, Cambridge, is a 'well intended' forgery by a preparator, for the belemnite guard has been artificially shaped to improve its appearance before being set in an artificial matrix in association with a genuine group of hooks. However, Huxley's interpretation appears to be correct and has been accepted by such later workers as Crick (1907), Naef (1922), and Jeletsky (1966).

Buckman (1879) described a specimen of a head of hooked arms from the Lower Lias, which he named *Belemnoteuthis montefiorei*. This specimen is in the collection of the British Museum (BMNH C5026) and the hooklets are identical with the types A, B, and C described here. However, in affinity this specimen seems to be *Belemnites* as suggested by Crick (1902) and not the *Belemnoteuthis* of Pearce (1842).

The most complete study of the arms of Liassic and other Jurassic dibranchiates is undoubtedly that of Crick (1907). He examined seventeen specimens of 'belemnite' arms in the British Museum collections and described and figured six of these specimens in detail in his paper. Crick concluded that the belemnites possessed six arms bearing rows of hooklets with swollen bases, as types A, B, and C, while *Belemnoteuthis* (= *Acanthoteuthis*) had eight or ten arms bearing hooklets with pointed bases. This latter form of hooklet is characteristic of fossil dibranchiates known from the Upper Jurassic Oxford and Kimmeridge Clays in Britain, and the lithographic stone of Solenhofen in Germany (Pearce 1842, Owen 1844, Mantell 1852, Crick 1897 and 1907).

Several of the standard textbooks on palaeontology (Zittel 1913, Woods 1946, and Piveteau 1953) figure dibranchiate cephalopod hooklets from Mesozoic sediments but give little idea of possible affinities of the various forms. Naef (1922) in his authoritative work on fossil dibranchiates figures and discusses various forms, including types from the Upper Lias of Holzmaden similar to types B and C of this paper, but is uncertain of any definite correlation of hooklet form with type of dibranchiate. Both Naef (1922, p. 219) and Jeletsky (1966, p. 138) disagree with Crick's (1907) interpretation of six-arm belemnites and suggest that they had eight or ten arms in common with the belemnoteuthids. Jeletsky (1966, p. 138) believes that all members of the order Belemnitida possessed arm hooklets.

From a detailed study of the literature and museum specimens it is here suggested that some broad association of hooklet form with three major groups of Mesozoic dibranchiate cephalopod may be possible. Members of the Belemnitidae may have had hooklet types A, B, and C as described here, characterized by a gentle curved shape and a swollen bifid base. Such forms are known mainly from the Lias (Huxley 1864, Crick 1907, Naef 1922, and Jeletsky 1966). Dibranchiates of the family Belemnoteuthidae may

have had gently curved or recurved hooklets with an elongate obliquely pointed base. This hooklet type is known from Upper Jurassic specimens (Pearce 1842, Owen 1844, Mantell 1852, Crick 1897, 1907, Hekker and Hekker 1955). Genera of the order Phragmoteuthida probably had hooklets of a belemnite type (Jeletsky 1966, p. 31). Separated hooklets of a variety of shapes are frequently found in microfaunas of Jurassic and Cretaceous age and are known as '*Onychites*' sp. (Quenstedt 1885, Naef 1922, Piveteau 1953, Hekker and Hekker 1955). Such hooklets probably belonged to other little-known members of the order Belemnitida as fossil teuthoid squids and sepoid cuttle fish seem to have been devoid of arm hooklets in Mesozoic seas (Jeletsky 1966). Therefore, the types of hooklets described in the earlier part of this paper would seem to have belonged to dibranchiate cephalopods of the family Belemnitidae, and not the family Belemnoteuthidae or the order Phragmoteuthida.

TABLE 1

Arms and arm hooklets of fossil belemnoids from the Lower Lias. Details from Woods (1946, fig. 169) and Crick (1907, pl. 23, figs. 1, 3, and 5).

Specimens	Number of arms	Total no. of hooklets	Hooklets per arm		Number of hooklets per arm of lengths		
			mean	max.	> 40 mm.	> 30 mm.	> 20 mm.
SM. J37812	8	211	29	34	32 (5)	0	17 (3)
BM. C3007	6	143	24	28	26 (3)	21 (3)	0
BM. 82895	4	123	31	36	31 (4)	0	0
BM. 47020	6	156	25	30	26 (2)	26 (2)	24 (2)
Approx. 'mean'	6	c. 150	27	32	29	23	20

Examination of published figures and museum specimens of 'belemnite' arms with hooklets (e.g. Woods 1946, fig. 169, and Crick 1907, pl. 23, figs. 1 to 6) has enabled observations to be made regarding the number of hooklets per arm, the total number of hooklets per belemnite individual, and the arrangement of hooklet types along the arms.

The varied state of preservation of specimens with arms from the Lower Lias makes detailed analysis very difficult. Crick (1907) showed that of the seventeen specimens in the British Museum collections only six were worthy of description, and of these six only three are considered sufficiently complete by the present author for detailed analysis (Table 1). Crick (op. cit.) showed that the belemnite arms varied in length, and that the hooklets were arranged in two parallel rows on the inner surface of the arms. In many of the known specimens the arms are either incompletely preserved or superimposed, so that it is impossible to be certain of the original arrangement of the arm hooklets. The specimens listed in Table 1, although varying in the number of arms, all possess arms that appear to be complete, as the hooklets are arranged in parallel rows, and are largest in the mid-length of each arm, gradually diminishing in size towards each end (Crick 1907, p. 271). From Table 1 it appears that the number of hooklets per arm varies with the length of the arm, but about thirty (fifteen pairs) hooklets per arm is an average number. Specimen SM. J37812 possesses eight distinct arms, and therefore confirms that there must have been eight or more arms in the belemnites in agreement with Naef (1922) and Jeletsky (1966). There must have been, therefore, at least 300 hooklets on an individual ten-armed belemnite in Liassic times.

The detailed arrangement of the hooklets along the arms can only really be seen on two of the specimens included in Table 1, Wood's fig. 169 (SM. J37812) and BMNH 82895 (Crick 1907, pl. 23, fig. 3). On these specimens the proximal hooklets are seen to be small examples of types A and B. The hooklets at mid-length of the arms are large examples of types B and C which decrease in size towards the distal end. This broad pattern of hooklet arrangement can be seen to a lesser extent on other less well preserved specimens (e.g. Crick 1907, pl. 23).

Significance of the gastric contents

(a) Feeding habits

Diet. The evidence of the gastric contents and coprolites suggests that Liassic ichthyosaurs fed mainly on fish and/or dibranchiate cephalopods. Among fish-eaters stomach contents were rarely preserved while coprolites are commonly found. A reverse situation possibly exists regarding dibranchiate eating forms, stomach contents being commonly preserved but coprolites rarely. Both these diets suggest that ichthyosaurs in Liassic seas were predators on nectonic not benthonic animals. If at least two distinct dietary habits were established amongst Liassic ichthyosaurs, they could be explained by either selective predation, or feeding at different levels in the sea as in the sperm whale (Clarke 1962, p. 186). Drevermann (1914, p. 42) has suggested that in Upper Jurassic seas, virtually toothless ichthyosaurs like *Ophthalmosaurus* may have fed exclusively on naked cuttle fish. The suggestion put forward in an earlier section of this paper that some Liassic ichthyosaurs fed mainly on belemnoids is made with some reservation, as the known fossil belemnoids from the Lias where arm hooklets and hard parts occur in association are few and none too well preserved. The similarity of the ichthyosaurs in mode of life and diet to odontocete Cetacea, especially the sperm whale, has been suggested by several workers (e.g. Buckland 1835, p. 227, Kukenthal 1892, Branca 1908, and Wiman 1946).

Volume of food eaten. In the previous sections it has been shown that the gastric contents contain $478,000 \pm 250,000$ hooklets, and that each belemnite probably had about 300 arm hooklets. The gastric contents described here, therefore, could represent between 760 and 2,430 digested individual belemnites. The undigested organic hard parts of these belemnites accumulated in the stomach, much in the same way as arm hooklets and beaks of modern dibranchiates accumulate in the stomach of the sperm whale. Akimuskina (1955) records 28,000 squid beaks, representing 14,000 squids, and Clarke (1962) records 4,000 beaks plus 28 undigested squids, representing 2,160 squids, found in the stomachs of sperm whales caught in the North Pacific and Atlantic respectively. The length of time of accumulation of these belemnoid hooklets in the ichthyosaur stomach is impossible to ascertain. It could represent several meals or a lifetime's accumulation. Judging from the length of skull and relative size of the various bones it is probable that the ichthyosaur described was only a young specimen. In this particular specimen, therefore, the gastric contents might represent a lifetime's accumulation.

Mode of feeding. Several workers (i.e. Buckland 1836 and Seeley 1880) have suggested that the ichthyosaurs were voracious feeders, where the prey was swallowed whole without mastication, as in the sperm whale (Clarke 1956 and Clarke 1962). In the

teuthophagous whales the presence or absence of teeth makes very little difference to the efficiency of feeding (Clarke 1956). If a parallel situation existed amongst dibranchiate-eating Jurassic ichthyosaurs, the presence or absence of teeth could not be explained purely in terms of diet as suggested by Drevermann (1914). The sperm whale frequently has facial scars from squid tentacles (Clarke 1956), suggesting that the squids were swallowed head first. If belemnoids were eaten in this manner by Liassic ichthyosaurs, biting of the heads would cause separation of the hooked arms from the body with hard parts. Further significance of this comment is discussed below.

(b) Digestive mechanism

The ichthyosaurs appear to have swallowed their prey whole into a large expandable stomach where all the digestive breakdown took place (Buckland 1836). Chyme, including softened fish and reptile bones, passed into the intestine, and then the indigestible material was defecated as coprolites. In outline this digestive process is similar to that of the sperm whale (M. R. Clarke, pers. comm.). Undigested dibranchiate remains, hooklets, and possibly beaks accumulated in the stomach as they could not be passed on. The reasons for this accumulation are difficult to understand. Possibly the process was a defence mechanism on the part of the ichthyosaur to protect the delicate tissues of the posterior part of the digestive system from damage by the sharp undigested hooklets. The gastric contents could represent a gravity accumulation of indigestible material on the ventral side of the stomach in a very fluid chyme, produced by the digestive breakdown of cephalopod tissue. Such an explanation would account for the pockets of quartz grains found on the ventral side of the gastric mass (Pl. 72, fig. 2). A very fluid chyme might not have been able to transport the undigested matter through the pyrolic valve, as undoubtedly occurred with the viscous chyme produced from the digested fish remains, now preserved as coprolites. A third possibility is that the hooklets gripped in the ventral stomach wall and formed an interlocking network, trapping the quartz grains. This last suggestion could explain why the gastric contents of this specimen were not dispersed before burial, despite the slight dismembering of the skeleton.

The accumulation of such remains raises a number of problems for the ichthyosaur which can only be answered by further analogies with the sperm whale. Did these remains accumulate to the detriment of the animal, perhaps blocking the digestive tract and causing death? In the sperm whale the accumulated squid beaks are periodically vomited from the stomach (M. R. Clarke, pers. comm.). *Ambergris* frequently contains squid beaks and so may also aid this regurgatory process. Such mechanisms as these may have existed in the ichthyosaurs to clear inconvenient accumulations of hooklets from the stomach.

If Liassic ichthyosaurs frequently ate belemnoid dibranchiates, as has been suggested, another problem arises concerning the digestion of the crystalline calcite guards. Modern teuthophagous cetaceans have little difficulty in digestion of the conchiolinic or weakly calcified 'pens' of squids by solution in the stomach, but densely crystalline guards of the belemnites are much more difficult to destroy, as witnessed by their abundance in Mesozoic clastic sediments. As gastric contents with belemnoid guards are rare, or unknown, in ichthyosaurs three possible explanations are suggested:

1. Heads were bitten off and so guards were not swallowed. This seems an unlikely mechanism as in reptiles and modern teuthophagous cetaceans prey is swallowed whole.

2. The body with guard, phragmocone, and proostracum separated from the head in the stomach and was regurgitated. The habits of the sperm whale give some support for this suggestion as regurgitation of squids frequently occurs on capture of the whales, and in the digestive process in the stomach the bodies and heads of the squids separate at an early stage (Clarke 1956 and Clarke 1962).

3. The guards were dissolved, or broken up by gastroliths and then dissolved, by the chemical environment of the stomach. Difficulties with this possibility are that gastroliths are unknown in ichthyosaurs, and a very acid stomach environment would be necessary to have dissolved dense primary crystalline calcite.

However, of these suggestions processes 2 and 3 would seem to be the more likely. Other possible explanations may simply be that the ichthyosaurs, as modern cetaceans, primarily ate naked dibranchiates, or chemical solution of guard posed no problem for the digestive mechanism of the Liassic ichthyosaur.

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JOHN E. POLLARD
Department of Geology
The University
Manchester 13

MANTLE CANAL PATTERNS IN *SCHIZOPHORIA* (BRACHIOPODA) FROM THE LOWER CARBONIFEROUS OF NEW SOUTH WALES

by JOHN ROBERTS

ABSTRACT. The brachiopod *Schizophoria verulamensis* Cvancara, from the Lower Carboniferous of the Gresford district, New South Wales, has distinctive mantle canal patterns in small, medium, and large specimens. The different patterns are interpreted as stages in the ontogeny and are thought to result mainly from the growth and enlargement of the genitalia.

Changes in the morphology of the canals in pedicle valves throughout six horizons in the Lower Carboniferous sequence show a trend, probably genetically controlled, towards the earlier maturity of the genitalia. The superimposition of larger or mature mantle canal systems on smaller or immature systems indicates that the canals are impressed by periodic resorption, and it is argued that this probably took place during the winter when there was a stable mantle canal system and little shell deposition. In large specimens there are connexions between the vascula genitalia, vascula media, and lateral canals in the pedicle valve, and between the vascula genitalia and vascula myaria in the brachial valve. It is suggested that the connexions may have increased the amount of oxygenated coelomic fluid circulating over the gonads, possibly causing them to ripen earlier.

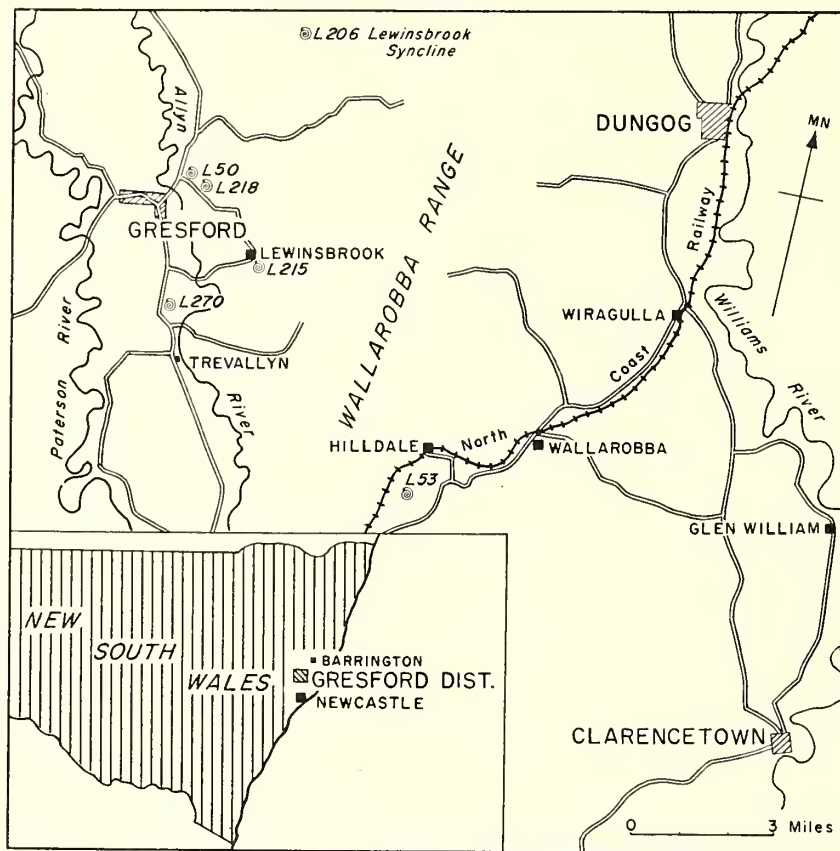
Pathological variations in the mantle canals are described, and it is shown that the canals are able to adjust to injuries or defects in the shell.

The mantle canals in living brachiopods are extensions of the body cavity into the mantle. Their function is mainly respiratory and in articulates they also act as receptacles for the gonads. In both living and fossil brachiopods the pattern of canals is frequently impressed on the inner surface of the shell, particularly that of older specimens. In fossil brachiopods impressions of the mantle canals are common in orthoids and strophomenoids, are rarely seen in the spiriferoids and chonetoids, and only recently have been observed in two species of productoids from the Lower Carboniferous of the Bonaparte Gulf Basin, northwestern Australia. As a result their use in systematics is limited.

Schuchert and Cooper (1932) described the morphology of the mantle canals in the orthoids and used the canal patterns as a basis for the separation of a new subfamily. Öpik (1934) further demonstrated their use in his study of the Clitambonitidina, and proposed a detailed terminology for the various parts of the mantle canal system. Williams (1956) was the first to present a comprehensive review of the mantle canal patterns in articulate brachiopods. He modified Öpik's terminology and showed that the mantle canal patterns in articulates could be referred to standard types which were probably derived from Cambrian forms. Williams (1956) and Williams and Rowell (1965) illustrated many different types of mantle canal patterns.

The present study deals with the morphology, development, and probable genetic changes in the mantle canals of the Lower Carboniferous orthoid *Schizophoria verulamensis* Cvancara (1958). Extremely well-preserved material has made possible the recognition of a sequence of young, mature, and old stages in the mantle canal system of *S. verulamensis*. These stages have in turn led to the recognition of a trend towards an earlier maturity of the reproductive system during the Lower Carboniferous, and a

method of impression or superimposition of the mantle canals which had not previously been recognised in the Brachiopoda. Because of the exceptionally fine preservation it has also been possible to recognize an intricate interconnexion between the various parts of the mantle canal system, a feature not recognized in Williams's and Rowell's treatment of mantle canal patterns.



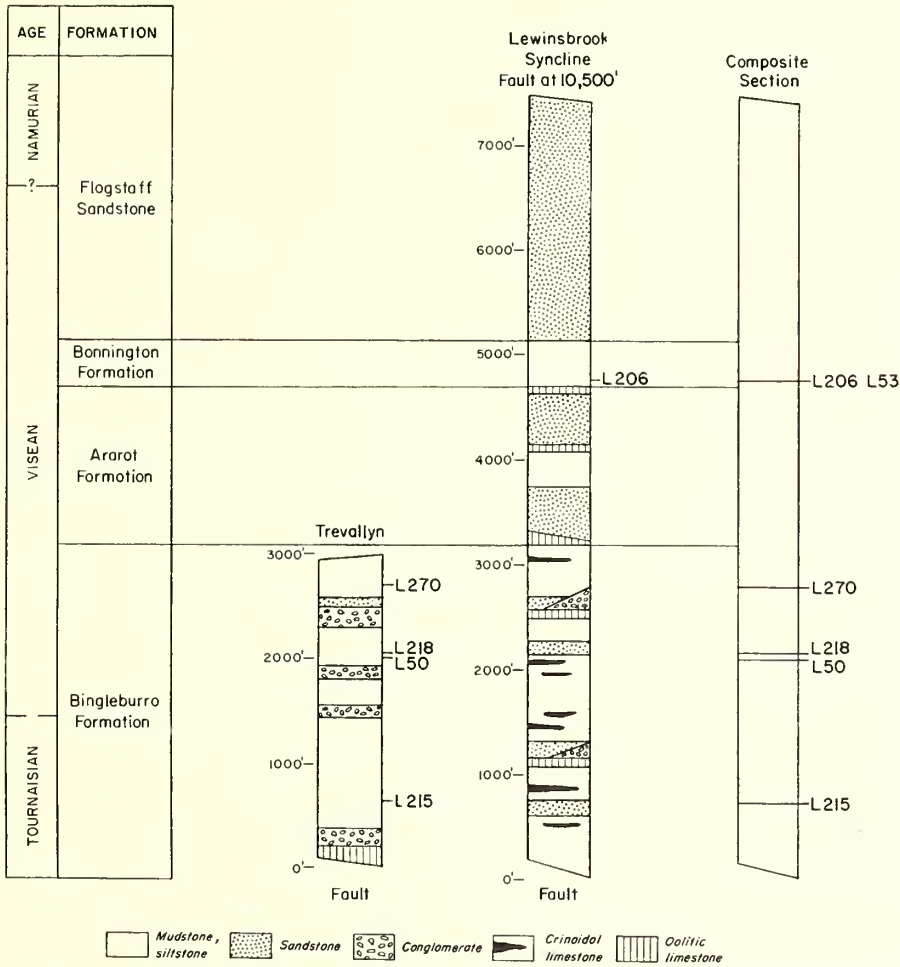
TEXT-FIG. 1. Locality of the Gresford District, N.S.W.

Schizophoria verulamensis Cvancara is one of the most common brachiopods in the Lower Carboniferous (Tournaisian and Viséan) of New South Wales, and has been collected from every known fossil horizon in the Gresford district, about 35 miles north-west of Newcastle (text-fig. 1). The majority of the specimens described in this paper are preserved in indurated grey siltstone; the rest occur in medium-grained lithic sandstone. They are exceptionally well preserved, and have very finely detailed impressions of the mantle canals and setal follicles. Internal moulds only are figured in the plates because the impressions of the canals, represented by ridges, are particularly prominent when illuminated by an oblique light source.

Schizophoria verulamensis is especially well represented in collections from the following localities (with grid references): L. 53 Greenhills (46609790), L. 206 Lewins-

brook syncline (46279968), L. 270 Trevallyn (45729864), L. 218 Gresford Quarry (45809912), L. 50 Gresford Quarry (45789913), L. 215 Lewinsbrook (46089882).

With the exception of L. 53 Greenhills, which is on the Paterson One-Mile Sheet, the grid references are taken from the Dungog One-Mile Sheet. The stratigraphic positions



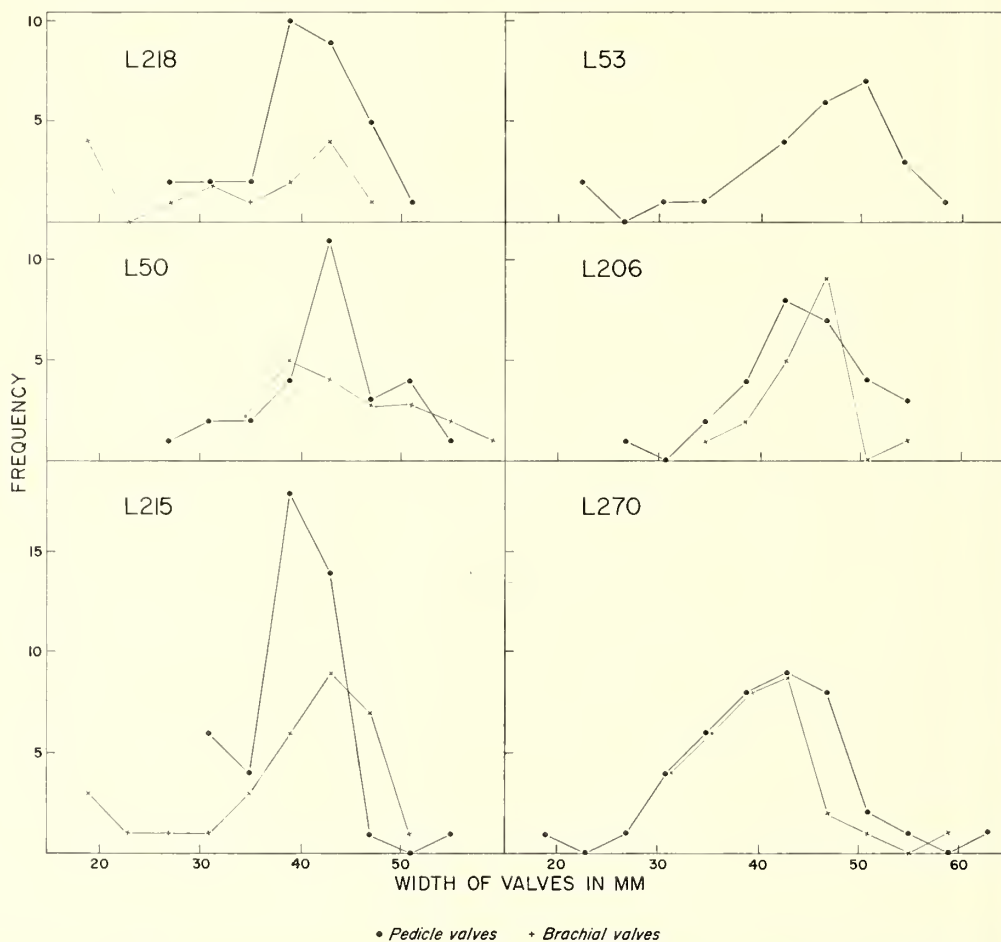
TEXT-FIG. 2. Diagrammatic stratigraphic sections of the marine rocks at Trevallyn and in the Lewinsbrook Syncline.

of the horizons are shown in text-fig. 2 on diagrammatic stratigraphic sections of the marine rocks in the north-western part of the Gresford district. All of the collections are housed in the Geology Department, University of New England, Armidale, N.S.W.

The stratigraphy of the Gresford district has been described by Roberts (1961 and 1965c) and the faunas by Roberts (1963, 1964, and 1965a and b), Campbell and Roberts (1964), and Brown, Campbell, and Roberts (1965).

The specimens of *Schizophoria verulamensis* were collected from a single horizon at each fossil locality except L. 53, where two horizons were sampled. An attempt was

made to collect randomly at each locality, and all the specimens collected were examined in the laboratory. Width-frequency plots for pedicle and brachial valves are given in text-fig. 3. The samples are characterized by the almost total absence of small specimens, and the presence of a large number of disarticulated valves, features which suggest that the populations had been affected by current action and sorting prior to burial.



TEXT-FIG. 3. Width-frequency polygons for *Schizophoria verulamensis* Cvcancara specimens from six localities in the Gresford district.

The post-mortem modification is also borne out by the unequal numbers of pedicle and brachial valves and small number of articulated shells collected from each locality. These figures are given in Table 1. The collection from L. 270 is the only sample having a comparable number of pedicle and brachial valves and also contains the greatest number of articulated shells, suggesting that it is perhaps the closest to a life assemblage.

Further evidence that most of the assemblages are death assemblages is provided by the occurrence, at L. 218, L. 270, and L. 206, of shell beds containing large numbers of

mature specimens of *Schizophoria* to the virtual exclusion of smaller specimens and other small species. The L. 53 horizon contains several other large species as well as *Schizophoria*, but also has very few small species. Smaller species and polyzoan debris accompany the *Schizophoria* specimens at L. 215 and L. 50.

TABLE 1

Locality	<i>Disarticulated valves</i>		<i>Articulated shells</i>
	<i>Pedicle valve</i>	<i>Brachial valve</i>	
L. 53	25	6	—
L. 206	28	18	1
L. 270	31	30	10
L. 218	30	23	1
L. 50	25	20	5
L. 215	54	31	7

MANTLE CANALS

The mantle canals in living brachiopods are situated in the mesenchyme layer of the mantle and are lined with ciliated epithelium. They are filled with coelomic fluid, which is rapidly circulated by the ciliated epithelium (Hyman 1959, p. 593), the circulation in some species being facilitated by a median ridge dividing the in- and out-flowing currents. The coelomic fluid contains free coelomocytes, including a spherical type which has a respiratory function and may be equivalent to a red blood corpuscle (Hyman 1959, p. 557). The pigment in the 'respiratory cells' absorbs oxygen and on reduction releases it to oxygenate the tissues.

The pattern of the mantle canals varies in different brachiopod groups (Williams 1956), and there is usually a different pattern in the pedicle and brachial valves. In most cases the canals originate as wide branches from the body cavity; some of these divide repeatedly until they extend to the proximal ends of the setal follicles around the edge of the mantle; other form sac-like receptacles and act as gonocoeles.

Most living brachiopods have a complicated system of mantle canals extending throughout the mantle, providing a large surface area through which oxygenation of the coelomic fluid can take place. An adaptation to increase the surface area of the mantle canals is illustrated by Williams and Rowell (1965, fig. 24) in which the mantle canals in the inarticulate *Glottidia* subtend gill ampullae into the mantle cavity.

In some fossil groups, however, the mantle canals have a relatively small surface area, and respiration may have been largely carried out by the lophophore. The lophophore in modern articulates has a plentiful supply of coelomic fluid provided by the coelomic canal and the small brachial canal (Williams and Rowell 1965, fig. 30). The small brachial canal gives off a branch to each of the filaments on the lophophore which have a large surface area and are ideally suited to respiration. Spiriferoids, for example, had narrow pinnate mantle canals with a small surface area combined with a large spiral lophophore. The lophophore probably had a large surface area suitable for oxygen exchange, was bathed in a stream of fresh water brought in by the moving filaments, and was an ideal organ for respiration as well as food gathering. Mantle canals appear to be poorly developed in the productoids, which probably also had a spiral lophophore

(Williams 1956, fig. 5 (6); Brunton 1966, figs. 8 and 9), and the lophophore may have acted as the main respiratory organ. Chonetoids occasionally exhibit mantle canals (Muir-Wood 1962, pl. 6, fig. 7), but they too probably used a spiral lophophore for respiration as well as for food gathering.

The mantle canals are also the receptacles for the gonads in living articulate brachiopods, and so the gonads are continuously bathed in oxygenated coelomic fluid.

Blood vessels, which are distinct from the mantle canals, extend from the body cavity into the mantle canals and run along the margins nearest the mantle cavity (i.e. along the inner margins of the mantle canals). These vessels, which are only seen in living brachiopods, follow all the branches of the mantle canals and extend to the margin of the mantle, and also form anastomosing blood sinuses to the gonads (Hancock 1859, pl. 55, fig. 1; pl. 63, fig. 1; and pl. 56, fig. 4). The blood system in brachiopods is an open system, the blood returning to the body cavity by way of tissue spaces. The blood itself is generally free of cells (Hyman 1959, p. 558) and consists of a colourless lymph-like fluid. Because the blood seeps back to the coelomic cavity before being recirculated it is probably coelomic fluid from which the coelomocytes have been filtered off. The blood system is responsible for the supply of nutriment to the organs within the body cavity, the gonads, and to the mantle, especially to the cells at the growing edge of the mantle. Waste products are probably transported by the blood as it filters through the tissues back to the coelome, where they are removed by the nephridia. The blood must also contain dissolved minerals, mainly calcium carbonate, for deposition as shell material by the cells at the growing edge of the mantle.

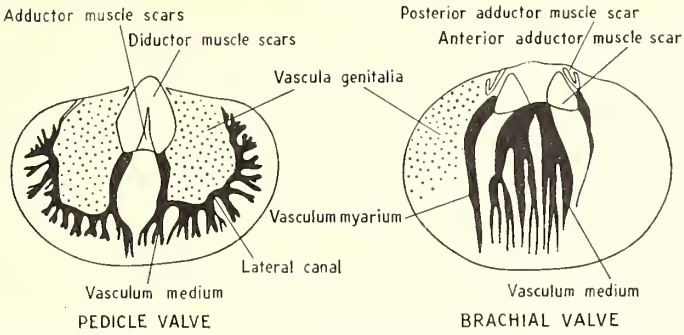
MANTLE CANALS IN *SCHIZOPHORIA VERULAMENSIS*

The morphology of the mantle canal impressions in both valves of *Schizophoria verulamensis* is shown in text-fig. 4. In the following description of the mantle canal system I propose to use the term 'canals' for the impressions of the mantle canals on the inner surfaces of the valves so as to avoid another descriptive term.

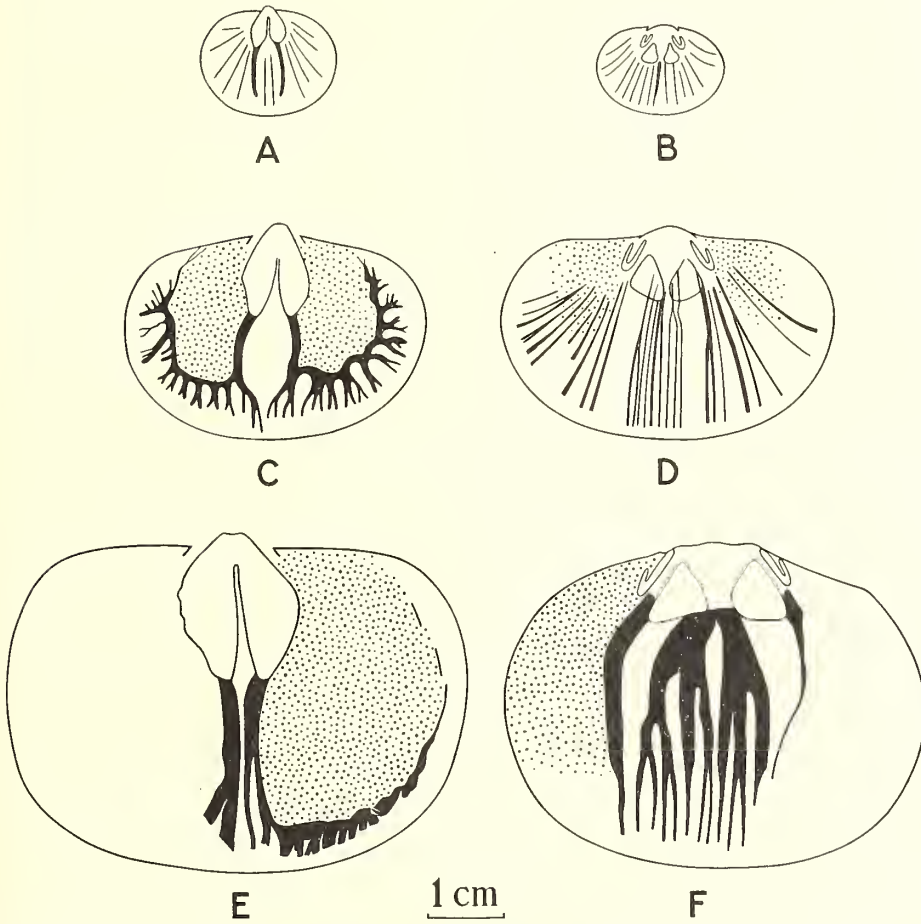
The mantle canals of small and apparently sexually immature specimens of *Schizophoria verulamensis* consist of small canals of *vascula media* and *vascula myaria* as well as a large number of narrower linear canals originating from the anterior and antero-lateral margins of the muscle field and extending to the margins of the valve (text-fig. 5 *a, b*). There is no differentiation of *vascula genitalia*.

In the pedicle valve the impressions of the *vascula media* arise from the anterior margins of the diductor muscle scars and extend with only minor branching to the front of the valve. An arcuate lateral canal such as that in older individuals (text-fig. 5*c*) does not appear to have been developed and the lateral margins of the valve were presumably supplied with coelomic fluid by the narrow linear canals extending from the body cavity.

Impressions of the mantle canals are less frequently preserved in brachial valves. Small brachial valves have canals of *vascula media* originating from between the inner margins of the anterior adductor muscle scars or, more rarely, from the inner parts of the adductor scars, and extending towards the front of the valve. The *vascula myaria* are simple, straight canals arising from between the anterior and posterior adductor muscle scars and extending towards the postero-lateral margins.



TEXT-FIG. 4. Morphology of the mantle canal impressions in *Schizophoria verulamensis* Cvancara.



TEXT-FIG. 5. Mantle canal patterns in *Schizophoria verulamensis* Cvancara showing the development from small to large individuals. The pedicle valve is on the left and the brachial valve on the right.

Larger, apparently sexually mature individuals (text-fig. 5 *c, d*) have an interconnected system of vascula genitalia in the pedicle valve (Pl. 74, fig. 3), an incipient system of vascula genitalia in the brachial valve (Pl. 74, fig. 6), and more complex vascula media and vascula myaria canals.

In the pedicle valve of mature individuals the main canals of vascula media are well separated from one another and are much broader and more deeply impressed than in the younger form. Each of the main canals branches distally, giving off a number of canals which run to the front of the valve, and an arcuate lateral canal which extends parallel with the margin of the valve to the hinge. The lateral canal has a crenulate pattern and at the peak of each crenulation gives off a major branch, which usually subdivides several times before reaching the margin of the valve. Towards the hinge the lateral canal is irregularly crenulate and terminates in a group of diverse branches. The vascula genitalia cover an area enclosed by the muscle field, the vascula media, and the inner margins of the arcuate lateral canals, and are connected by numerous branches with the vascula media and lateral canals; the significance of these connexions will be dealt with below.

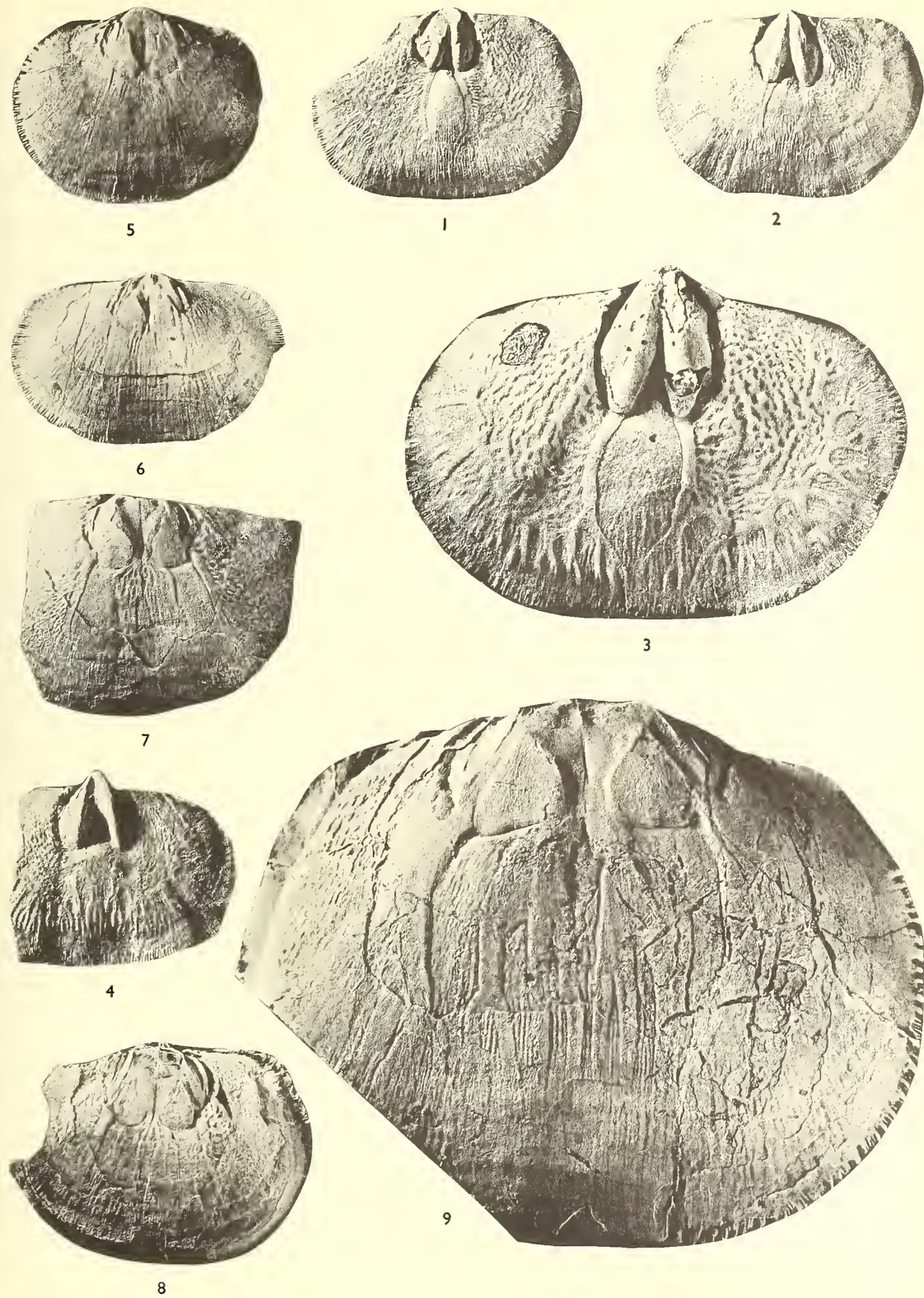
The vascula genitalia in brachial valves having the same size and presumably the same age as mature pedicle valves do not appear to be as strongly impressed as those in the pedicle valve. The genital markings consist of pit-like depressions or incipient interconnected canals on the postero-median parts of the valve, and give rise to numerous branching canals, similar to those of the vascula media and vascula myaria, which extend to the lateral margins (Pl. 74, fig. 6). There are up to ten canals of vascula media, and ten canals of vascula myaria extending with variable bifurcation towards the anterior margin. Both the vascula media and vascula myaria leave tracks on the anterior adductor muscle scars.

In the largest and probably gerontic specimens (text-fig. 5 *e, f*) the mantle canal system is frequently more strongly impressed on the inner surface of the shell and is characterized by even broader main canals and an expansion of the vascula genitalia.

EXPLANATION OF PLATE 74

Schizophoria verulamensis Cvcancara

- Fig. 1. $\times 1$. F.7145a. Internal mould of pedicle valve showing the connexions between the vascula media and vascula genitalia; L. 215 Lewinsbrook.
- Fig. 2. $\times 1$. F.7145r. Internal mould of pedicle valve; note the truncation of the narrow canals by the main canals of vascula media; L. 270 Trevallyn.
- Fig. 3. $\times 2$. F.4677a. Internal mould of pedicle valve showing a sexually mature mantle canal system superimposed over an immature system; L. 215 Lewinsbrook.
- Fig. 4. $\times 1$. F.8036. Internal mould of pedicle valve showing a third canal of vascula media extending to the front of the valve; L. 50 Gresford Quarry.
- Fig. 5. $\times 1$. F.7147q. Internal mould of brachial valve showing a sexually immature pattern of narrow linear mantle canals; L. 270 Trevallyn.
- Fig. 6. $\times 1$. F.7141a. Internal mould of brachial valve showing the early development of the vascula genitalia; L. 215 Lewinsbrook.
- Fig. 7. $\times 1$. F.7153b. Internal mould of mature brachial valve showing the connexion between the vascula genitalia and the vascula myaria; L. 50 Gresford Quarry.
- Fig. 8. $\times 1$. F.7153c. Internal mould of a mature brachial valve; note the connexion between the vascula genitalia and the vascula myaria; L. 50 Gresford Quarry.
- Fig. 9. $\times 2$. F.7153a. Internal mould of an old brachial valve; note the narrow canals emerging from beneath the wide superimposed canals of vascula media; L. 50 Gresford Quarry.





In the pedicle valve the main vascula media canals are close together and branch distally, the arcuate lateral canals are closer to the margin than in younger specimens, and the vascula genitalia have the same ramifying canals as those in mature specimens, covering almost the entire inner surface of the valve (Pl. 75, figs. 4–7).

The canals of vascula media in the brachial valve are usually wider than in smaller specimens but do not appear to have significantly altered their positions. The vascula myaria are also broader and run straight to the antero-lateral margins, or are bent inwards at their distal extremities. Many small branches along the outer margins of the vascula myaria provide a connexion with the vascula genitalia. The genitalia have the same morphology as those in the pedicle valve. They cover broad flabellate areas on the lateral and postero-lateral parts of the valve, but have a smaller area than the genitalia on the pedicle valve because they are confined by the vascula myaria.

A system of narrow linear canals at the margins of mature shells (Pl. 74, figs. 1–3, 9; Pl. 75, figs. 1, 2) are continuous with small branching canals in the middle part of the shell (viz. the small canals between the vascula media in Pl. 74, fig. 3). These small branching canals are interpreted as impressions of a juvenile mantle canal system, and hence their distal parts are regarded as impressions of mantle canals, probably impressions of the termination of the canals at the proximal ends of the setal follicles. These impressions were apparently continuously recorded by a process of differential thickening at the margin. The linear canals are joined by branches of a superimposed mantle canal system (see below), indicating their function as a canal rather than the trace of a setal follicle. Had they been merely traces of setal follicles they would intercalate as new setae were introduced around the margin; when they increase, these canals branch (Pl. 74, fig. 3; Pl. 75, fig. 3).

Changes in the mantle canals. In the pedicle valve the main canals of vascula media extending in front of the muscle field can be divided into three intergrading morphological types (text-fig. 6):

- A. Canals convex outwards and widely separated.
- B. Canals straight and widely separated.
- C. Canals straight and close together.

It has been shown above that the A and B types of canals typify small- to medium-sized individuals and C type canals larger individuals, and hence the different shapes of the vascula media can be explained as stages in the ontogenetic development of the individual. Accompanying the change from the A to C types of canals is the enlargement of the complex network of the vascula genitalia, and it is suggested that this enlargement within the mesenchyme layer of the mantle gradually forced the vascula media canals together and the lateral canals to move towards the margin as the shell became older. Specimens having each of these types of canals are present in all of the horizons in the Gresford district.

This explanation of the development of the canals does not account for their distribution as outlined in Table 2, unless evolution has taken place.

An analysis of Table 2 is simplified if it is realized firstly that the C type canal is that seen in the largest specimens, and secondly that the L. 53 sample is dominated by large specimens (text-fig. 7). Table 2 shows a decrease in A type canals and an associated

increase in B type canals from the oldest to the youngest horizons. This trend could be explained in at least two ways: as the expression of the ontogeny, as outlined above, in which sampling errors gave the impression of a genetic change, or as a true genetic change towards the earlier maturity of the genitalia.

An examination of the width-frequency polygons (text-fig. 3) shows that the samples are essentially the same in terms of size distribution, except for L. 53. Also, the specimens from the highest stratigraphic horizon with B type canals are about the same size as specimens from the lower horizons characterized by A type canals. In the absence of genetic change the specimens having the B type canals should have been larger.

TABLE 2

	Canal types		
	A	B	C
L. 53 Greenhills	Occasional	30%	70%
L. 206 Lewinsbrook Syncline	25%	75%	occasional
L. 270 Trevallyn	65%	35%	occasional
L. 218 } Gresford Quarry	65%	35%	occasional
L. 50 }			
L. 215 Lewinsbrook	70%	30%	occasional

More conclusive evidence in favour of the genetic change is available from younger horizons (probably middle to upper Viséan) at Barrington, N.S.W., in which moderate to large specimens of *S. verulamensis* have mainly straight, sub-parallel (or B type) canals (Cvancara 1958).

The earlier maturity of the genitalia would have increased the number of larvae produced by each individual and probably significantly increased the *S. verulamensis* population to one of even greater dominance during the Viséan.

Superimposition of mantle canals. In mature specimens of *Schizophoria verulamensis*, particularly in pedicle valves, the greater part of the mantle canal system is superimposed over small radial canals. The small canals originate from the body cavity frequently branch, and run irregularly towards the front of the shell. In mature valves the posterior parts of these canals (viz. the narrow branching canals between the main vascula media in Pl. 74, fig. 3) are interpreted as the traces of juvenile mantle canals.

EXPLANATION OF PLATE 75

Schizophoria verulamensis Cvancara

Fig. 1. $\times 2$. F.7152a. Internal mould of pedicle valve showing narrow canals extending from the front of the muscle field and being truncated by the superimposed mature mantle canal system; L. 50 Gresford Quarry.

Fig. 2. $\times 2$. F.7146k. Internal mould of pedicle valve; L. 270 Trevallyn.

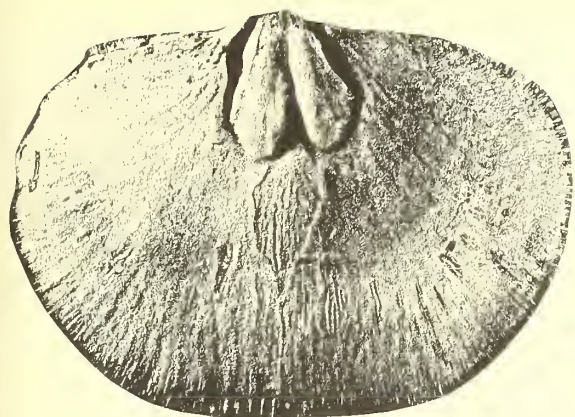
Fig. 3. $\times 2$. F.4677b. Internal mould of pedicle valve; L. 215 Lewinsbrook.

Fig. 4. $\times 1$. F.7144o. Internal mould of an old pedicle valve; L. 53 Greenhills.

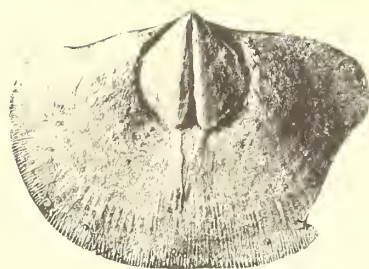
Fig. 5. $\times 1$. F.4784. Internal mould of an old pedicle valve with C-type vascula media and large areas of vascula genitalia; L. 53 Greenhills.

Fig. 6. $\times 1$. F.7145b. Internal mould of an old pedicle valve; L. 270 Trevallyn.

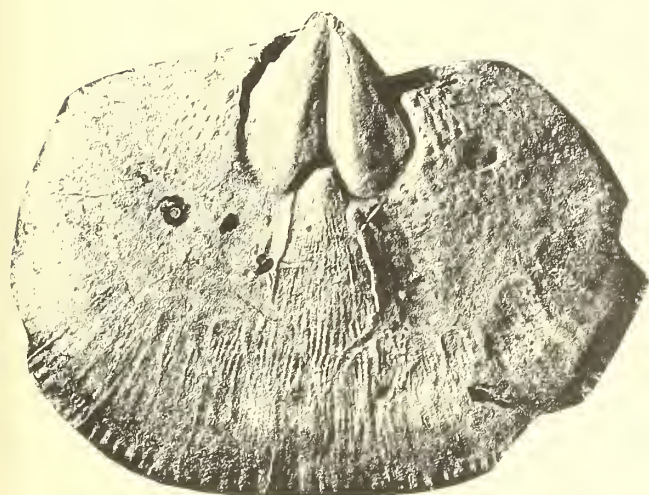
Fig. 7. $\times 1$. F.7146c. Internal mould of an old pedicle valve with large vascula genitalia, C-type vascula media and the lateral canals situated close to the margin; L. 270 Trevallyn.



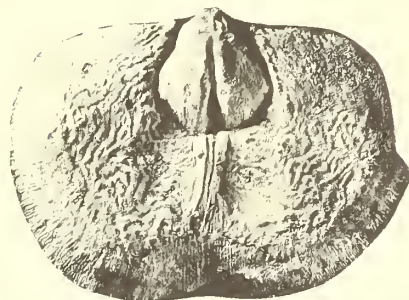
1



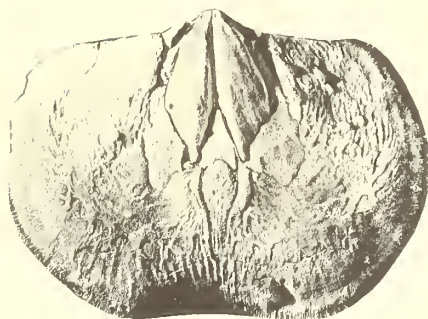
4



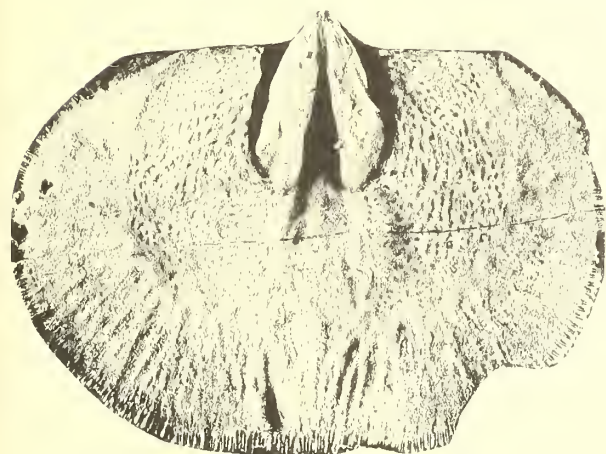
2



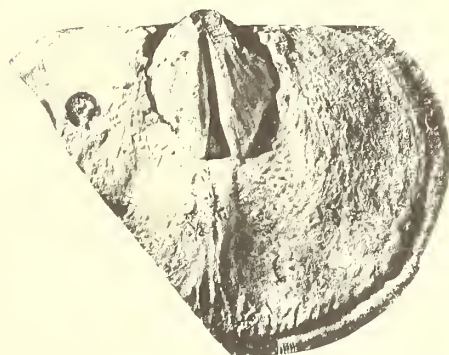
5



6



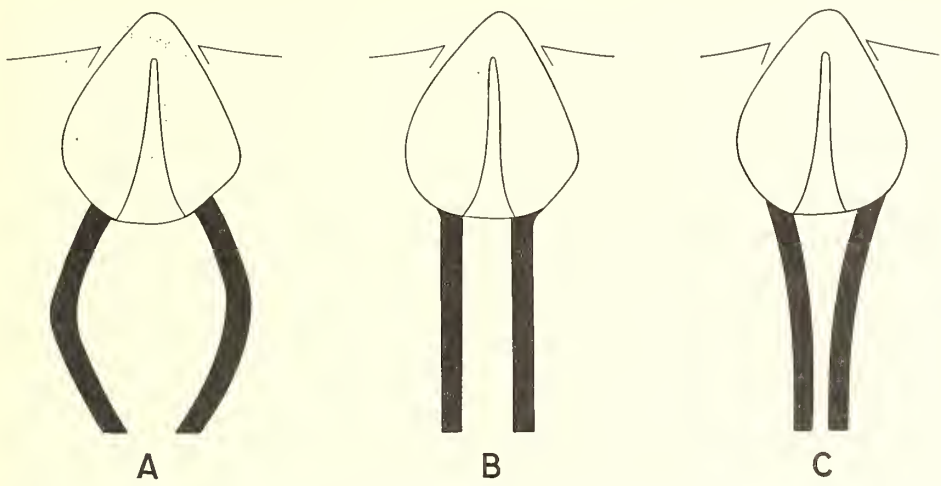
3



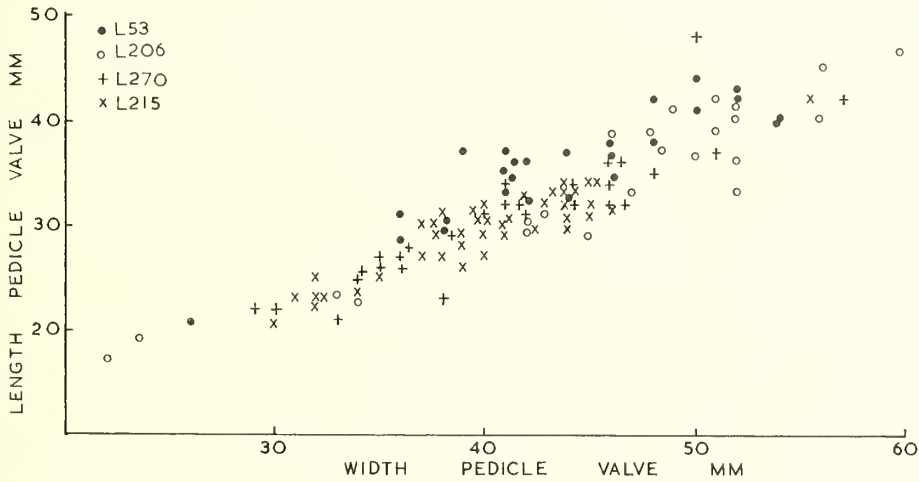
7



Because all the canals were connected to the bases of the setal follicles (Williams and Rowell 1965) these juvenile canals are continuous with the traces, recorded at the margin, of the termination of the mantle canals at the setal follicles.



TEXT-FIG. 6. The three types of vascula media canals in the pedicle valve of *Schizophoria verulaeensis* Cvcancara.



TEXT-FIG. 7. Scatter diagram of length plotted against width for pedicle valves of *Schizophoria verulaeensis* Cvcancara from L. 215 Lewinsbrook, L. 270 Trevallyn, L. 206 Lewinsbrook Syncline, and L. 53 Greenhills.

In mature pedicle valves impressions of the small canals extend from the front of the muscle field between the large canals of vascula media, branching as they run towards the front of the valve (Pl. 74, fig. 3; Pl. 75, figs. 1, 2). In the middle and mid-anterior

parts of the valve they are truncated by superimposed larger canals: viz. the inner branch of the right-hand vasculum medium on the specimen in Plate 74, fig. 3 in which small canals extend on either side of a branch of the superimposed larger canal. Near the margins, the large canals join with the narrow linear traces left by the mantle canals at the ends of the setal follicles, and extend to the depressions left by the setal follicles. The junction between these canals results from both systems supplying the same setal follicles at the margin; the small linear marks were impressed as the shell grew, and the larger canals, which had been formed by the modification of the smaller ones, were impressed at a later time.

The superimposition of the mantle canal systems is less clear in the brachial valve. One large specimen, however, has a system of narrow linear canals beneath broad canals of *vascula media* (Pl. 74, fig. 9). The U-shaped branch on the left hand side of the *vascula media* truncates at least six of the narrow canals, and other narrow canals emerge from beneath the sites of bifurcation of the larger canals and are apparently continuous with the traces of the canals at the bases of the setal follicles.

The two main systems (i.e. the younger and older systems) described above are interpreted as impressions of the mantle canals at two different periods during the life of the shell, probable before and after sexual maturity. Because of the impression of a large or mature system on top of a smaller and probably immature system it is inferred that the major part of the canal system was impressed at certain well-spaced intervals instead of being continuously recorded on the inside of the shell.

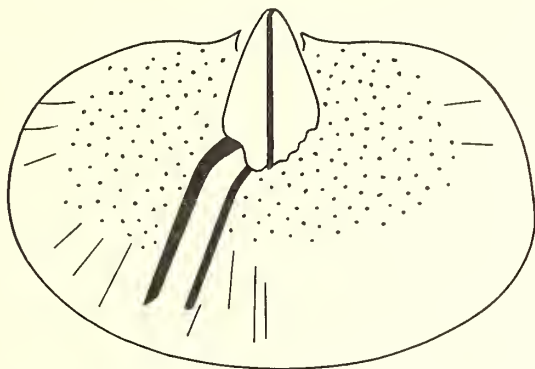
Williams (1956, p. 273) thought that mantle canals were impressed on the inner surface of the shell by differential secretion of shell material by the outer epithelium covering the canals. In *S. verulamensis* this mechanism may have been responsible for the continuous impression of the distal parts of the canals at the margin, but it could not have been responsible for the impression of the main part of the mantle canal system, because there are two and sometimes three systems superimposed over one another, unless rapid differential secretion took place at specific times; this is unlikely because it means that rather than being gradually thickened the shell would have been periodically rapidly thickened.

A more convincing explanation is that the outer epithelium over the mantle canals resorbed the shell material at specific times. Resorption is most likely to have taken place during the periods of limited shell growth when the mantle canal system had a stable morphology. During periods of rapid growth there would have been continuous reorganization of the mantle canals at the mantle edge and the development of additional setal follicles at the growing margin. To maintain efficient circulation to the margin the main canals of *vascula media* and *vascula myaria* would have enlarged by reorganizing the connective tissue in the mantle and coalescing with smaller canals. Many modern shallow-water marine organisms, particularly molluscs, cease depositing shell during the colder months of the year (Epstein and Lowenstam 1954), and hence it is reasonable to assume that the winter was the most likely time for the retardation of shell deposition and the impression of the mantle canals in *S. verulamensis*.

Abnormal mantle canals. In the pedicle valve figured in Plate 74, fig. 4, the left-hand canal of *vascula media* divides a short distance in front of the muscle field, giving a third main canal extending to the median anterior part of the valve. All three canals

branch in a similar manner to those in other valves. Functionally this additional large branch may have provided a greater supply of coelomic fluid to the growing edge of the front of the mantle. The two outer canals of *vascula media* give off arcuate lateral canals.

Another specimen showing an abnormal development of the *vascula media* (text-fig. 8) has impressions of the two main canals of *vascula media* arising from the anterior margin of the left diductor muscle scar and running, parallel with one another, to the antero-lateral part of the valve. There is no canal originating from near the right diductor scar, presumably because of some injury or functional defect to that side of the body cavity, and the *vascula genitalia* extend in front of the muscle scar. The



TEXT-FIG. 8. Pathological pedicle valve of *Schizophoria verulamentis* Cvancara showing the two main canals of *vascula media* extending from the left diductor muscle scar, and the *vascula genitalia* extending in front of the right diductor muscle scar.

preservation is too poor to trace the junction of the right-hand canal with the right lateral canal. This variation indicates a certain adaptability in the organization of the mesenchyme layer of the mantle, and supports the arguments put forward above that major reorganizations took place within the mantle during the development of the species. Other features probably associated with this deformity are a deep furrow on the antero-median part of the left diductor muscle scar and an exceptionally narrow median ridge which does not expand anteriorly.

In a large pedicle valve (Pl. 75, fig. 6) branches from the arcuate lateral canal in the posterior part of the valve, instead of extending normal to the margin of the valve, turn posteriorly and run almost parallel with the margins, diverging only slightly from the main lateral canal. In other valves (Pl. 74, fig. 3) only the posterior-most branches of the lateral canal turn and run more or less parallel with the canal.

Connexion between the mantle canals. The description and figures of mantle canals of fossil brachiopods given by Williams (1956) and Williams and Rowell (1965) suggest that each of the three pairs of extensions of the coelomic cavity into the mantle—the *vascula media*, *vascula myaria*, and *vascula genitalia*—is a discrete unit, unconnected with other canals.

Larger specimens of *Schizophoria verulamensis* with well-preserved mantle canals have vascula media and arcuate lateral canals possessing well defined inner and outer margins. The vascula genitalia contained within the arc of the lateral canals is connected by many fine branches with the main vascula media canals and the arcuate lateral canals, the connexions varying from narrow constricted branches (the branches on the right-hand vasculum medium of the specimen in Pl. 74, fig. 3) to broad canals (the connexion with the right-hand lateral canal on the same specimen). In another specimen (Pl. 74, fig. 1) the branches into the vascula media canals are more pronounced and have a herringbone pattern. As well as being connected with the vascula media, the vascula genitalia are presumably connected directly with the coelomic cavity adjacent to the muscle-field.

There is no connexion with the vascula media in the brachial valve, but instead the vascula genitalia are linked with the main canals of vascula myaria (Pl. 74, figs. 7, 8). The branches are comparable with those in the pedicle valve and appear to extend along the entire outer margin of the vascula myaria canals.

Similar connexions occur in Ordovician orthid brachiopods described by Cooper (1956) (see *Chaulistomella magna* (Schuchert and Cooper), pl. 70, fig. 21; and *Mimella globosa* (Willard), pl. 89, figs. 10, 12, 14). One other possible example of an interconnected system in *Schizophoria* is given by Pocock (1966, fig. 17), who figured a specimen of *S. striatula* (Schlotheim) in which lateral branches arise from the vascula myaria and extend towards the vascula genitalia.

This type of interconnexion between the genitalia and the other mantle canals is apparently unknown in modern brachiopods. The interiors of modern brachiopods figured by Hancock (1859) show that the genitalia are either situated in the mid-part of a sac-like mantle canal, such as that in *Terebratulina caputserpentis* Linné (Hancock 1859, pl. 53, figs. 1, 2), or lie within the narrow canals of vascula genitalia or vascula media as in *Macandrevia cranium* (Müller) (Hancock 1859, pl. 53, fig. 4). In specimens with sac-like mantle canals, closest to those in *Schizophoria*, the vascula media and lateral canals are simply the lateral extremities of the gonocoel; they have no inner walls, and hence differ from the discrete canals in *S. verulamensis*. There are no connexions with the network of genitalia, but the genitalia are bathed in coelomic fluid. In *S. verulamensis*, coelomic fluid must have actually passed along the tubular network of vascula genitalia.

The connexion of the vascula genitalia with other canals in *S. verulamensis* probably increased the circulation of oxygenated fluid over the gonads, the fluid coming from the vascula media and lateral canals (or the vascula myaria in the brachial valve) as well as from within the vascula genitalia itself. The gonads in brachiopods without interconnected canals are oxygenated only by the coelomic fluid contained within the vascula genitalia, and sometimes the vascula media, meaning that there is probably less oxygenated fluid passing over them. Additional aeration could be responsible for the formation of larger gonads and possibly for a faster rate of production of sex cells, and it may also cause them to ripen earlier. In the modern brachiopod *Terebratulina caputserpentis*, already mentioned above, the gonads are bathed in the coelomic fluid of a large sac-like gonocoel, which is probably an even more efficient method of aeration.

The interconnexion of the canals seems to be a favourable attribute, and on a purely morphological basis it would seem that a system, such as that in *S. verulamensis*, would

have been more efficient for respiration and reproduction than, for example, a more restricted, discrete system such as that in the recent brachiopod *Fallax* (Williams and Rowell 1965, fig. 23D). Some of the respiratory functions of the mantle could, however, have been taken over by the lophophore in other brachiopod groups, so that there was less need to develop an interconnected system and the mantle canals acted as repositories for the gonads and as an accessory respiratory system.

The present work shows that a closer examination of living brachiopods is desirable to see if any species have an interconnected mantle canal system like that in *S. verulamensis* and other orthid brachiopods.

Interpretation of the mantle canals. The development of the mantle canals in *S. verulamensis* can be interpreted as follows. During the first period of growth, probably about one year, the shell was sexually immature and had a relatively undifferentiated system of mantle canals. In the first winter, when there was little shell growth, narrow linear canals including vascula media and vascula myaria were impressed on the inner surface of the shell, probably by resorption (Pl. 74, fig. 5). During the following summer the shell grew rapidly and became sexually mature. The rapid growth and the introduction of many setal follicles at the mantle edge, combined with the growth of the gonads, resulted in the reorganization of the mantle canal system. In the pedicle valve the vascula media became wider and developed complex lateral canals, and the vascula genitalia changed from narrow linear canals to a network of ramifying channels which branched with one another and with the main branch and lateral canal of the vascula media (Pl. 74, fig. 3). The changes in the brachial valve were not as marked; the canals of vascula media and vascula myaria becoming wider, and vascula genitalia becoming pitted near the postero-medial part of the valve and also having wider canals extending to the lateral margins (Pl. 74, fig. 6). These canals were impressed during the second winter, when the shell was about two years old.

The changes in mature individuals, especially the development of the lateral canals and the network of vascula genitalia in the pedicle valve, must have resulted in a complete reorganization of the connective tissue in the mantle as well as the introduction of many blood vessels to the new canals and the genitalia. According to Hyman (1959, p. 533) the connective tissue of living brachiopods consists of a 'homogeneous material containing stellate mesenchymal cells that may unite into loose networks'; the mesenchyme was thus probably easily modified to allow the introduction of new or larger canals.

Further growth in the following summer resulted in an increase in size, the enlargement of the muscle-field, and a thicker shell, especially at the posterior. In the pedicle valve the vascula genitalia increased enormously in size, forcing the main vascula media canals close together (Pl. 75, figs. 4-7) and the lateral canals towards the margin, so that the impressions of the mantle canals covered almost the whole inside of the valve. In the brachial valve the vascula media and vascula myaria canals became wider and the vascula genitalia developed a ramifying network similar to that in the pedicle valve (Pl. 74, figs. 7, 8, 9). These enlarged canals were probably impressed during the third winter.

Little is known about the rate of growth and maturity of modern brachiopods. Rudwick (1962, p. 334; 1965, p. H209) suggested that modern articulate brachiopods

can reach sexual maturity after two or three years, and that they live for as long as seven or eight years or even longer. Amongst the inarticulates *Lingula* is sexually mature after a year or a year and a half (Chuang 1959), and *Glottidia* after only six to nine months (Paine 1963). It is therefore reasonable to suggest that *S. verulamensis* became sexually mature at about two years old, and that the mature mantle canal system was impressed during its second winter. Mantle canals of older individuals cover almost the entire surface of the shell and leave no room for the expansion of the vascula genitalia, so that after about the third year the mantle canals became stable and could not be modified during further growth of the shell. There is no indication of how long the largest shell lived.

SUMMARY AND CONCLUSIONS

The morphology of the mantle canals in *Schizophoria verulamensis* Cvancara changes during ontogeny, mainly because of the growth of the gonads. The canals start in immature specimens as narrow linear canals over the inner surface of the valves and, with the growth of the gonads, are later modified in larger specimens into several major feeder canals which distribute coelomic fluid from the body cavity to the margins of the shell, around the areas of genitalia. In the largest shells the genitalia cover the greater part of the inner surface of the valves and have enlarged to such an extent that the large distributive canals have been forced together in the middle of the valve, or moved outwards towards the margins. The pedicle valve is affected earlier by the growth of the genitalia than the brachial valve.

An analysis of the distortion to the main vascula media caused by the enlargement of the vascula genitalia in pedicle valves from six horizons throughout the Lower Carboniferous sequence indicates a trend, probably genetically controlled, towards the earlier maturity of the genitalia.

The main part of the mantle canal system was impressed periodically by the resorption of shell beneath the mantle canals rather than by differential secretion as suggested by Williams (1956). Resorption most likely took place during the winter when there was limited shell growth and a stable mantle canal system, recording several distinct mantle canal patterns during the development of the individual.

Larger specimens of *S. verulamensis* have the vascula genitalia connected by numerous small branches with the vascula media and lateral canals in the pedicle valve and the vascula myaria in the brachial valve. This type of connexion has not been observed in recent brachiopods. It is thought to have increased the circulation of oxygenated coelomic fluid over the gonads, and may have been responsible for their earlier ripening.

The mantle canals in pathological specimens indicate that not only was modification possible during ontogeny, but the mantle canal system could also be adapted to the effects of injuries or defects in the shell during life.

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JOHN ROBERTS

Bureau of Mineral Resources, Geology
and Geophysics
Canberra City, A.C.T.
Australia

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ON '*DENDROCRINUS*' *CAMBRIENSIS* HICKS, THE EARLIEST KNOWN CRINOID

by DENIS E. B. BATES

ABSTRACT. *Dendrocrinus cambriensis* is re-described from new material and referred to *Ramseyocrinus* gen. nov., and placed in the family Eustenocrinidae.

THE crinoid remains described by Hicks from the lower Ordovician rocks of Ramsey Island and the adjacent mainland of Wales are the earliest yet reported, and, as such, might be expected to yield significant information on the origin of the class. Several writers (Moore 1950, p. 32, Ubaghs 1953, p. 744, Regnéll 1960, p. 172) have referred to their early stratigraphical occurrence, and Ramsbottom (1960, p. 5) has re-investigated Hicks's specimens, without being able to add significantly to Hicks's information. Unfortunately none of Hicks's specimens shows the posterior side, and hence the anal tube was unknown. The writer has had the opportunity of examining the extensive collection of material from Ramsey Island made by Dr. F. J. North for the National Museum of Wales, kindly made available by Dr. D. A. Bassett, and has based his description on specimens from it.

Class CRINOIDEA J. S. Miller 1824

Subclass INADUNATA Wachsmuth and Springer 1881

Order DISPARATA Moore and Laudon 1943

Family EUSTENOCRINIDAE Ulrich 1924

Monocyclic crinoids with a slender cylindrical crown about equal in diameter to the stem; calyx composed of three (?) to five basals, four radials, and an equal-sized infer-radial; four arms, branching isotomously; infer-radial bearing a series of unbranched quadrate plates presumably supporting an anal sac.

Genus *Ramseyocrinus* gen. nov.

Diagnosis. A genus of the Eustenocrinidae with a four-lobed stem composed of columnals of irregular thickness; basals probably three in number, separated by well-developed sutures.

Type species. *Dendrocrinus cambriensis* Hicks 1873.

Discussion. The described species of *Eustenocrinus* have a round smooth column, with two alternating sets of thin columnals, one set twice as thick as the other. The five basal plates are all imperfectly fused one to another. In *Ramseyocrinus* there are, apparently, fewer basals, and the sutures between them are as well defined as those between the radials.

[Palaeontology, Vol. 11, Part 3, 1968, pp. 406-9, pl. 76.]

Ramseyocrinus cambriensis (Hicks)

Plate 76, figs. 1-5

1873 *Dendrocrinus cambriensis* Hicks, p. 50, pl. 4, figs. 17-20.1960 *Iocrinus?* *cambriensis* (Hicks) Ramsbottom, pp. 5-6, pl. 3, figs. 9-11.

Diagnosis. Basals low, over twice as wide as high; rectangular radials wider than high, and highly convex; nine or more primibrachs, arms branching at least three times.

Type specimens. The syntypes (Ramsbottom 1960, p. 5) are preserved in the Sedgwick Museum, with some gutta-percha impressions in the Geological Survey Museum. Ramsbottom's description is mainly based on a specimen preserved in the British Museum (BMNH E3). The author has also discovered in the Sedgwick Museum the counterpart mould of one of Hicks's syntypes, and the specimen now bears the numbers SM 16739a-b. The description below is mainly based on a specimen from the National Museum of Wales, preserved as counterpart moulds (29 308 G296 and G318).

Type locality. All the specimens figured by Hicks come from the Porth Gain Beds of Bay Ogof Hên, Ramsey Island (Pringle 1930, p. 12), although specimens are recorded from near Llanveran Farm, on the mainland near Pen Berry. No specimens have been seen or found by the writer from the latter locality.

Description. Cup slightly wider than high, sides flaring slightly upwards, surface of plates smooth. Basals apparently not more than four in number, and probably only three, just less than half the height of the calyx and over twice as wide as high, pentagonal, with the upper surfaces concave, and the lower surfaces sharply bent inwards between the petals of the stem. Radials four in number, quadrangular, wider than high, with convex lower and concave upper surfaces, highly convex, especially towards their lateral margins. Anal series commencing with an infer-radial similar in width and convexity to the radials, but only half their height, the succeeding three plates of the anal series similar in size and height. The radials and first primibrachials almost equal in height to the infer-radial and the succeeding two plates of the anal series. Lowermost brachials not interlocking and probably not included in the cup.

Primibrachs nine to twelve, wider than high, almost circular in cross-section, with a deep narrow ventral groove, secundibrachs four to nine, as high as wide; tertibrachs seven or more; quadribachs at least eight; arms branching isotomously at least three times.

Stem wide, petaloid, four lobed, the lobes proximally almost parallel-sided with deep indentations, distally becoming less marked so that the stem becomes rectangular in cross-section; columnals of irregular height.

Discussion. Moore and Laudon (1943, p. 26) described the two lowermost plates in each ray of *Eustenocrinus* as infer-radial and super-radial, homologizing them with the compound radials of genera such as *Ectenocrinus* (op. cit., fig. 3). However, in a later paper (1950, p. 30) Moore has proposed a simpler nomenclature, regarding the lowermost plate in each ray (excepting that beneath the anal tube) as radial, and the plates above and incorporated in the cup as fixed brachials. The latter procedure is followed here.

The chief differences from the described species of *Eustenocrinus* are in the form of the stem and the number of basals, which warrant separation of the Welsh species into a new genus. There are at least three basals, one of which, on the anterior side, may be formed

from two plates fused together and showing traces of the suture between them (Pl. 76, fig. 1). In addition *E. springeri* (Ulrich 1924, p. 99) has arms which bifurcate only once, and its diameter at the top of the basals appears to be less than at either the base or top of the cup (op. cit., fig. 14A). *E. milleri* (Wetherby 1880, p. 153) has the radial plates higher than wide, with a thickening of their upper extremity which gives the species a somewhat swollen appearance at the top of the calyx.

Eustenocrinus was considered by Moore and Laudon (1943, p. 25) as the most primitive member of the homo-synbathrocrinids, the major stock of the Disparata. Stratigraphically, however, it post-dates the earliest members of that stock, and hence is not itself the ancestor. The features considered by Moore to be primitive include the steep-sided conical cup, the convex base showing the lowest plates, isotomous arm branching, and the lack of any fused super and infer-radial plates. The occurrence of *Ramseyocrinus* at the base of the Ordovician, and its similar structure, further strengthens Moore's claim for this stock to be the ancestor of the Disparata.

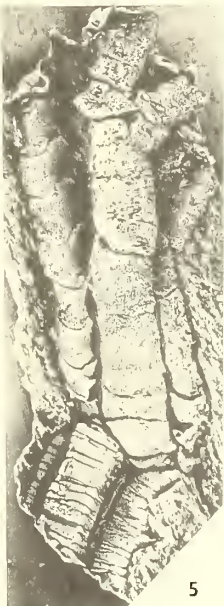
The most striking features of *Ramseyocrinus* are the four-lobed stem and the four arms. It was hoped that *Ramseyocrinus* would prove to be a possible ancestor for the whole class Crinoidea, but these features indicate that it post-dates the splitting up of the ancestral crinoid stock into at least the sub-classes Inadunata and Flexibilia. Most other contemporary or older pelmatozoans have a well-developed five-fold symmetry, and thus it is likely that the Eustenocrinidae arose from an ancestor having five arms, one arm being replaced by an anal tube. Thus the Eustenocrinidae must first have lost the right posterior arm during the late Cambrian and then regained it during the early Ordovician, if they were, in fact, ancestral to the bulk of the Disparata. That this happened is questionable; it seems more probable that the Eustenocrinidae constitute an early simplified offshoot from the Disparata.

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EXPLANATION OF PLATE 76

- Ramseyocrinus cambriensis* (Hicks) from the Porth Gain Beds of Bay Ogof Hên, Ramsey Island. All photographs are of latex casts, whitened with ammonium chloride. None has been retouched.
- Figs. 1–3. Specimen 29 308 G296/G318 (Nat. Museum of Wales). 1. Anterior view, showing stem of irregular columnals, and two (?) basal plates partially fused together, $\times 5.8$. 2. Posterior view, showing the anal tube, two of the four (?) basals, and food grooves on two of the arms, $\times 5.5$. 3. Stem viewed from below, showing the four lobed cross-section, $\times 4.5$.
- Figs. 4–5. Syntype, specimen SM. 16739a–b (Sedgwick Museum, Cambridge). 4. Posterior (?) view, $\times 2.0$. 5. Anterior (?) view, $\times 3.1$. The basal and radial plates cannot be positively identified, nor can the anal series, which may be missing.



BATES, *Ramseyocrinus cambrensis* (Hicks)

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DENIS E. B. BATES
Department of Geology
University College of Wales
Aberystwyth

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REVISION OF TWO UPPER CAMBRIAN TRILOBITES

by A. W. A. RUSHTON

ABSTRACT. *Conocoryphe? bucephala* Belt, 1868, from the Upper Ffestiniog and Lower Dolgelly Beds of Wales, and possibly England, is re-illustrated; the pygidium is described for the first time; the species is transferred from the Olenid genus *Beltella* to which it was referred by Lake (1919) to *Parabolinoides* Frederickson, a genus widely known in the approximately contemporaneous *Conaspis* Zone in the U.S.A.

Sphaerophthalmus major Lake, 1913, though regarded by Henningsmoen (1957) as of questionable validity, is distinguishable from other species of *Sphaerophthalmus*; *S. major* occurs in England, Wales, and Sweden, and probably in Norway and eastern Canada, in the Zone of *Peltura scarabaeoides*.

IN his monograph on the Olenidae, Henningsmoen (1957) commented on the two Upper Cambrian trilobite species *Conocoryphe? bucephala* Belt and *Sphaerophthalmus major* Lake, but for lack of data was unable to frame a diagnosis for either. In connexion with work on the Cambrian faunas from the Institute of Geological Sciences Merevale No. 1 borehole (Rushton, 1966), I examined the type-material of both these species including material from the following museums: British Museum (Natural History) (BM), Geological Survey Museum (GSM), Oxford University Museum (Ox), and the Sedgwick Museum, Cambridge (SM). The terminology used in the description below is that of Henningsmoen (1957).

Family PARABOLINOIDIDAE Lochman Genus PARABOLINOIDES Frederickson 1949

Type species (by original designation). *Parabolinoides contractus* Frederickson 1949.

Parabolinoides bucephalus (Belt 1868)

Text-fig. 1; Plate 77, figs. 1–10, 11?

- 1868 *Conocoryphe? bucephala* Belt, p. 10, pl. 2, figs. 1–6.
- 1873 *Conocoryphe Williamsonsii* Salter, p. 12 [Not *Conocoryphe Williamsonsii* Belt, 1868].
- 1919 *Beltella bucephala* (Belt); Lake, p. 106, pl. 12, figs. 11–15.
- 1919 *Beltella verisimilis* (Salter) [*partim*]; Lake, p. 107, pl. 13, figs. 4, 5 only.
- ? 1927 *Beltella?* sp. nov. Cobbold, p. 557.
- ? 1930 *Beltella* cf. *bucephala* (Belt); Stubblefield, p. 57.
- 1957 *Olenus? bucephalus* (Belt 1868); Henningsmoen, p. 111 (with further synonymy).

Lectotype (selected by Henningsmoen 1957, p. 111). The original of Belt's plate 2, fig. 1. The only specimen extant which can be considered as this original is BM I 7578 from the Upper Ffestiniog Beds near Dolgelly, shown here on Plate 77, fig. 7; it is the only relatively large and complete specimen in Belt's collection, is the same size as his figure, and also agrees in being rather obscure in the posterior part of the shield. It is assumed that the figure is restored.

Remarks on the material studied. The specimens of *Conocoryphe? bucephala* collected by Belt and now in the British Museum (Natural History) and the Geological Survey

Museum show the effects of flattening, crushing, and deformation to varying extents: the lectotype is obliquely compressed and the preglabellar field is crushed on to the anterior extension of the doublure of the slightly displaced free cheek; the cranidia in Plate 77, figs. 3 and 4, are laterally and frontally compressed respectively, and that shown in fig. 1 is crushed flat but seems to be relatively undistorted. The glabella of the type specimen of *Conocoryphe williamsoni* Salter *non* Belt (Pl. 77, figs. 10a and b) is crushed on to the hypostoma, and the preglabellar field on to part of the free cheek, as in the lectotype of *Parabolinoides bucephalus*; the free cheeks are displaced backwards and inwards relative to the cranium and the pygidium is steeply inclined relative to the thorax, but otherwise the specimen is good, being but little flattened and deformed.

In an attempt to determine the original proportions of *P. bucephalus* the method suggested by Henningsmoen (1960, p. 207) was applied to two mature cranidia on one of Belt's slabs of Upper Ffestiniog Beds (GSM Za 4843) which satisfy the necessary conditions except that one is somewhat larger than the other. The calculation indicates that the original ratio of length to breadth of the cephalic axis was 4:3, which is in good agreement (less than 5 per cent. difference) with the ratios obtained from the apparently undeformed specimens shown in Plate 77, figs. 1, 6, and 10a; in contrast, direct measurement of the obviously deformed specimens in figs. 3 and 4 gives ratios of 2.0:1 and 0.9:1 respectively.

Description. Lake's description of the species is mainly correct but it requires some amplification, particularly in the account of the cranium.

Cephalic axis prominent, tapered, rounded in front, breadth three-quarters of length; S1 weak or distinct, long, oblique backwards, straight or slightly convex; S2 weak, short, less oblique; a few specimens show traces of S3, as stated by Belt (1868, p. 10); the appearance of the glabellar furrows varies much according to the state of preservation. Occipital furrow deepest medially, composite; occipital ring apparently without node or spine. Frontal area one-third to nearly half as long as cephalic axis; border-furrow slightly bowed forwards and, in some specimens, with a weak median in-bend; anterior border crescentic or subtriangular, longer at the mid-line than the preglabellar field. Eye-ridges distinct or weak. Eyes opposite S2 or L2. Inter-ocular cheeks half or less than half as wide as the glabella at the eye-line; post-ocular cheeks rounded postero-laterally, slightly narrower than the occipital ring. Pre-ocular facial sutures straight, divergent forwards to the border-furrow, strongly convergent over anterior border; post-ocular facial sutures divergent, slightly convex.

Free cheek with broad border and long anterior extension of the doublure (Pl. 77, fig. 8). Ventral sutures unknown.

There are twelve thoracic segments in the type-specimen of *Conocoryphe williamsoni* Salter and twelve or thirteen in the lectotype of *C. ? bucephala*, in which the joint between the thorax and pygidium is not very clear. The pleural tips are pointed and the axis lacks nodes except in young specimens.

Pygidium poorly known; pygidial axis with about four rings (including terminal); pleural regions with about three pleural and two interpleural grooves, three pairs of marginal spines and a striated doublure (Pl. 77, fig. 10b).

Young specimens in Belt's collection have a convex glabella which, compared with adult specimens, is larger in proportion to the rest of the cranium (Pl. 77, fig. 9).

Measurements in mm.

	SM A3095	BM 59284	BM It 2585
Length of cranium	11.0	10.0	6.1
Width of cranium	17.2	16.1 (est.)	9.0
Length of cephalic axis	c. 7.6	7.2	4.2
Width of cephalic axis	5.8	5.3	3.2

The lectotype is about 34 mm. long; SM A3095 is about 30 mm. long (restored).

Remarks. I agree with Lake (1919) in regarding Salter's *Conocoryphe williamsoni* as a synonym of Belt's *C.? bucephala*. Compared with *C.? bucephala* the glabella of *C. williamsoni* seems to be slightly smaller in proportion to the rest of the cranium but this may be because in *C. williamsoni* it is preserved convex (except where crushed on to the hypostoma), whereas in the relatively undeformed specimens of *C.? bucephala* it is 'spread' by flattening and crushing. Otherwise, so far as the species can be compared, they agree quite well. The small cranium collected by Stubblefield (1930) from Bentleyford Brook in Shropshire is slightly flattened compared with young specimens in Belt's material and has a less prominent anterior border, but is otherwise very similar. The specimens collected by Stubblefield from concretions in Comley Brook, Shropshire (Cobbold 1927, p. 557) and considered by him to be the same species as the Bentleyford cranium are very small but may provisionally be retained as *Parabolinoides* cf. *bucephalus*.

I have not seen the specimens from the Ffestiniog Beds illustrated by Lake (1919) as belonging to the Tremadoc species *Beltella verisimilis* (Salter), but from the illustrations they appear to be laterally compressed specimens of *Parabolinoides bucephalus*.

Generic position. The chief features of *Conocoryphe? bucephala*—the tapered glabella with oblique furrows and rounded front, wide anterior border, small eyes close to the glabella, the course of the facial suture and the spinose pygidium—are those of *Parabolinoides* Frederickson.

Belt's original reference to *Conocoryphe?* followed Salter's example in using the name for what would now be called ptychoparioid trilobites. Subsequent writers (Reed 1900; Lake 1919; Henningsmoen 1957) agreed in assigning *P. bucephalus* to the Olenidae, but the wide cephalic border and divergent pre-ocular sutures are not typical of that family. Nevertheless, *P. bucephalus* otherwise resembles late *Olenus* species such as *O. cataractes* Salter which, however, has more thoracic segments and stronger glabellar furrows;

EXPLANATION OF PLATE 77

Figs. 1–10. *Parabolinoides bucephalus* (Belt). 1. Cranium, Ffestiniog Beds near Penmaenpool, Merioneth, $\times 2\frac{1}{2}$, BM 59284. 2–5. Deformed crania, Upper Ffestiniog Beds near Dolgelly (Belt Collection), $\times 2\frac{1}{2}$; GSM Za4844, BM I 7580, BM I 7588, BM I 7590 respectively. 6. Crushed cranium with part of thorax; Ffestiniog Beds? $\times 2\frac{1}{2}$, BM It 2585. 7, 8. Lectotype and free cheek, Upper Ffestiniog Beds near Dolgelly (Belt Collection), $\times 2\frac{1}{2}$, BM I 7578, BM I 7583. 9. Convex immature cranium, probably this species, $\times 5$, BM 58499. 10. Complete specimen (type specimen of *Conocoryphe williamsoni* Salter), Lower Dolgelly Beds, Rhiwfelyn SM A3095; 10a, $\times 2\frac{1}{2}$; 10b, view of pygidium, $\times 5$. 11. *P.* cf. *bucephalus* (Belt); immature cranium from Orusia Shales (Lower Dolgelly Beds) in tributary of Bentleyford Brook, Shropshire, $\times 5$, GSM D2655.

Photographs by Mr. C. Friend.



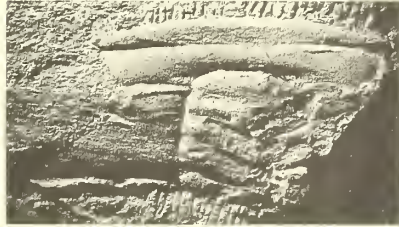
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2



3



4



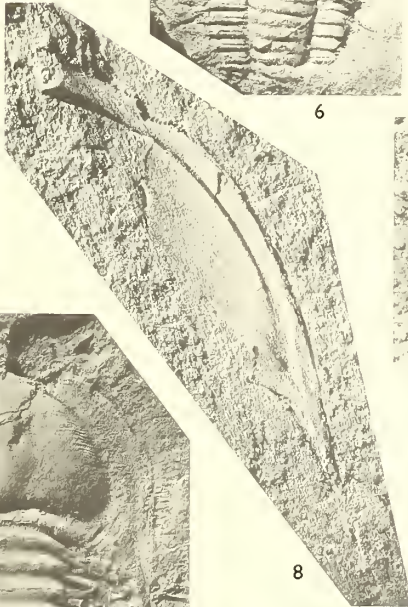
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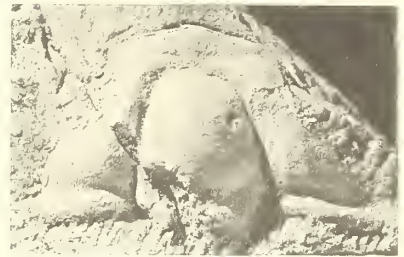
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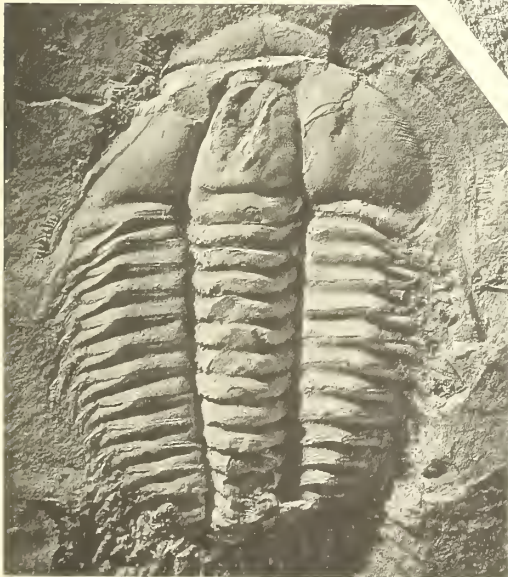
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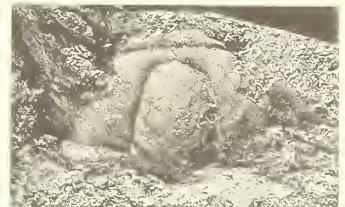
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9



10a

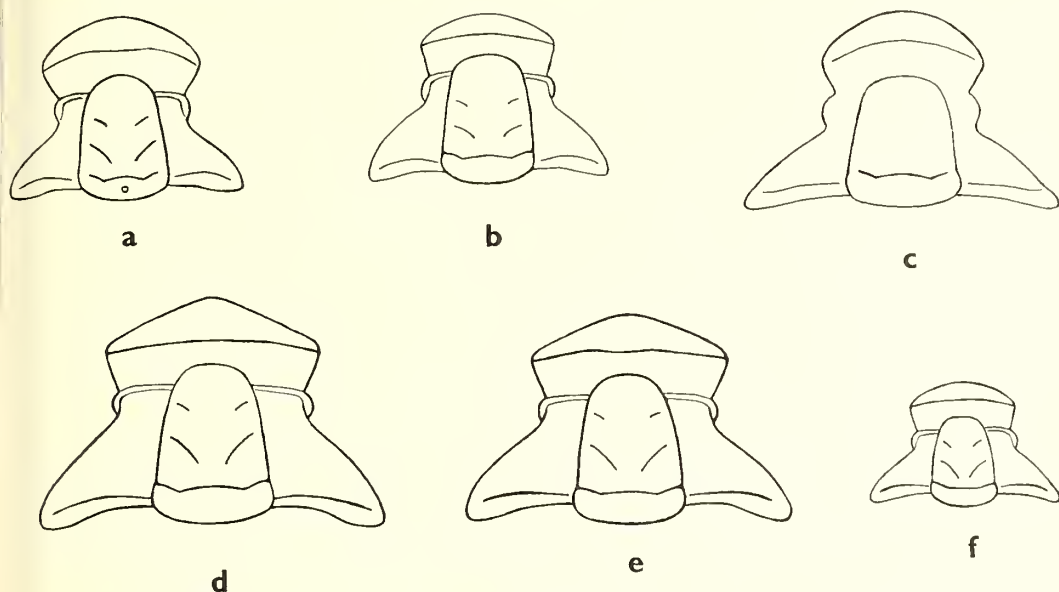


11



10b

species of the (typically Tremadoc) olenid genus *Beltella* Lake differ in having truncate pleural tips and an entire pygidial margin. *Leptoplastides* Raw, which is related to *Beltella* (Henningsmoen 1957, p. 265) but has spinose pleurae, differs from *P. bucephalus* in having axial spines and a different type of free cheek. *Beltella solitaria* Westergård (1922, pl. 14, fig. 1) has a less prominent anterior border and a truncate glabella, and seems to be a true Olenid.



TEXT-FIG. 1. Diagrammatic drawings of cranidia of *Parabolinoides* species, about $\times 2\frac{1}{2}$. (a) *P. contractus* Frederickson (after Frederickson 1948). (b) *P. hebe* Frederickson (after Frederickson 1948). (c) *P. palatus* Berg (after Berg 1953). (d-f) *P. bucephalus* (Belt), restored from various specimens.

P. bucephalus is placed in *Parabolinoides* rather than any other genus of the Parabolinoididae such as *Maustonia* Raasch in Lochman or *Taenicephalus* Ulrich and Resser in Walcott because the post-ocular sutures are convex rather than sinuous (see Lochman in Harrington *et al.* 1959, p. O272). *Bernia* Frederickson which has convex post-ocular sutures is considered a synonym of *Parabolinoides* by Bell and Ellinwood (1962, p. 398).

Comparison with other species (text-fig. 1). *Parabolinoides bucephalus* differs from other species of *Parabolinoides* in having the inter-ocular cheeks about half as wide as the glabella, whereas in other species they are only about one-third as wide. The most similar species are *P. contractus* Frederickson (1949) which, however, also differs in having a longer frontal area and an occipital node, and *P. hebe* Frederickson which has a relatively short anterior border and a more truncate glabella. *P. palatus* Berg (1953) has a relatively short, square glabella and more transverse post-ocular sutures. *P. ? cordillerensis* Lochman (1950) has relatively very narrow inter-ocular cheeks and somewhat sinuous post-ocular sutures.

Occurrence. *Parabolinoides bucephalus* has been found in North Wales and possibly in Shropshire at horizons at or near the top of the *Olenus* Zone and in the *Parabolina spinulosa* Zone (Upper Ffestiniog and Lower Dolgelly Beds).

The specimens in Belt's collection are all labelled 'Upper Ffestiniog, Dolgelly' and in his account of the species Belt (1868) mentions the localities Gwern-y-barud (near Penmaenpool), Mynydd Gader, and near Craig-y-Dinas. G. J. Williams collected *P. bucephalus* at the same horizon in Nant Cistfaen and on Trinant, near Arenig (Lake 1919, pp. 107, 109). Mr. S. W. Hester of the Geological Survey has collected a specimen identified by Stubblefield as *Beltella* cf. *bucephala* from the basal Lower Dolgelly Beds at Ogof Ddu, one mile east of Criccieth, Caernarvonshire. The type of *Conocoryphe williamsoni* Salter is stated by Lake (op. cit., p. 107) to be from the 'Upper Lingula Flags' (= Dolgelly Beds) at Rhiwfelyn in the Upper Mawddach Valley; a variety of horizons is exposed near Rhiwfelyn (Wells 1925, map, pl. 32) but the lithology of the specimen agrees with that of the Lower Dolgelly Beds which yield *Parabolina spinulosa* (Wahlenberg).

Immature cranidia of *Parabolinoides* cf. *bucephalus* have been collected from a septarian nodule from Comley Brook, south Shropshire (Cobbold 1927, pp. 556-7) where they were associated with *Parabolina spinulosa* and *Orusia lenticularis* (Wahlenberg). In a section at Bentleyford Brook a single immature cranidium was collected near the base of a 63-ft. thickness of micaceous shales which, at higher horizons, yielded also *Orusia lenticularis* and *Parabolinites*? [*Parabolinella*] aff. *williamsonii* (Belt).

Apart from *P. bucephalus*, recorded species of *Parabolinoides* are confined to the *Conaspis* Zone in the central parts of the United States of America (Lochman and Wilson 1958, see text-figs. 9, 10, 11). If, as has been suggested, the top of the *Elvinia* Zone is not higher than the top of the *Olenus* Zone (Rushton 1967), *P. bucephalus* and the American species of *Parabolinoides* occur at about the same horizon.

North Welsh succession	European Zones	North American Zones
Lower Doglelly	<i>Parabolina spinulosa</i>	<i>Conaspis</i>
Ffestiniog		
	<i>Olenus</i> f	<i>Elvinia</i>
Upper Maentwrog	e (6 sub-zones a-f)	
	d	

Family OLENIDAE Burmeister
Subfamily LEPTOPLASTINAE Angelin
Genus SPHAEROPHTHALMUS Angelin 1854

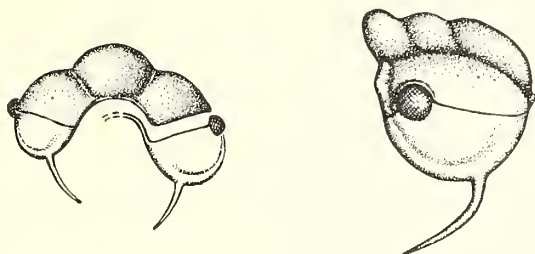
Type species (subsequently designated by Linnarsson 1880). *Trilobites alatus* Boeck, 1838.

According to Henningsmoen (1957, p. 211) there are four species of *Sphaerophthalmus*, all occurring in the Upper Cambrian *Peltura* Zones of the North Atlantic Province. He

lists *S. alatus* (Boeck), *Olenus humilis* Phillips 1848, *S. majusculus* Linnarsson 1880, and *S. major* Lake 1913. Henningsmoen discussed the nomenclature of the species; his conclusions may be summarized as follows:

1. In 1880 Linnarsson stated that *Olenus humilis* Phillips was a junior synonym of *Sphaerophthalmus alatus* (Boeck). Henningsmoen showed that this was a mistake, the species being distinct.

2. Other workers accepted Linnarsson's statement; one such was Lake (1913) who figured and described material from Phillips's type-area for *Olenus humilis* under the name *S. alatus* (Boeck). Henningsmoen suggested that the name *humilis* should be revived for *S. alatus* of Lake (not Boeck). Lake (op. cit.) also described a new species, *S. major*.



TEXT-FIG. 2. Reconstruction of cephalon of *Sphaerophthalmus humilis* (Phillips) showing attitude of free cheek, $\times 10$, anterior and lateral views. Cranium after Westergård.

3. Westergård (1922) likewise figured Phillips's species under the name *S. alatus* and he tentatively assigned a second species to *S. major* Lake; he also re-illustrated *S. majusculus* Linnarsson. Henningsmoen pointed out that although the Scandinavian specimens of '*S. major*' should be referred to *S. alatus* (Boeck) the same was not necessarily true of the type-material of *S. major*.

The morphology of Sphaerophthalmus. The cranidia of species of *Sphaerophthalmus* are convex so that the differences between specimens preserved in limestone and those in shale are quite important, as can be seen in the figures given by Westergård (1922, pl. 13, figs. 9–35). For example, the transversely arched anterior border, when flattened, becomes an emargination in dorsal view (Westergård 1922, pl. 13, figs. 20 and 23), and the post-ocular cheeks are bent up from their original steeply down-sloping attitude so that the width of the cranium is increased. When the cranium is flattened the facial suture describes an elongated S-shape, but when preserved convex the course is, in dorsal view, curved anteriorly and nearly straight behind and, in side view, arched up at the palpebral lobe.

The free cheek of *Sphaerophthalmus* bears a hemispherical eye which projects beyond the general line of the facial suture; it appears that this can only fit under the arched palpebral lobe if the free cheeks slope steeply, as I have attempted to show in text-fig. 2. As the cheek spine is bent down in relation to the general plane of the margin of the free cheek it seems that, in life, these spines curved under the cephalon (text-fig. 2), in which position they would prevent the trilobite from crawling on the sea floor; Henningsmoen (1957, p. 78) has suggested that *Sphaerophthalmus* may have been a strong swimmer.

Sphaerophthalmus major Lake 1913Text-fig. 3*b*; Plate 78, figs. 1–8

- 1913 *Sphaerophthalmus major* Lake, p. 77, pl. 8, figs. 7, 9–13; ? non fig. 8.
 1949 *Sphaerophthalmus major* Lake; Edmonds, p. 60.
 1952 *Sphaerophthalmus major* Lake; Hutchinson, p. 90, pl. 4, fig. 17?; non fig. 16 [= *Ctenopyge fletcheri* (Matthew)].
 1957 *Sphaerophthalmus major* Lake 1913; Henningsmoen, p. 217.
 1957 *Sphaerophthalmus humilis* (Phillips 1848) [*partim*]; Henningsmoen, pl. 22, figs. 7, 11?, 15 only.
 1957 *Sphaerophthalmus minor* [*sic*]; Henningsmoen, p. 218 (error for *S. major*).

Lectotype. As lectotype I select the cranidium GSM 8903 (Pl. 78, fig. 2) illustrated by Lake (1913, pl. 8, fig. 7) which was collected from the White Leaved Oak Shales at White Leaved Oak, Malvern, and presented to the Geological Survey by Miss M. Lowe.

Other material. Apart from BM I 14849 (the original of Lake's pl. 8, fig. 10) which has not been seen, all of Lake's syntypes have been examined and are considered to be conspecific except possibly I 14851 (the original of Lake's pl. 8, fig. 8); this consists of two free cheeks, probably of a *Ctenopyge* species, and a thorax, possibly of *S. major*, upside-down and back-to-front in relation to them. Topotype material in the collections of the Geological Survey Museum, the Sedgwick Museum, the Oxford University Museum, and the British Museum (Natural History) has also been examined.

Diagnosis. A species of *Sphaerophthalmus* with palpebral lobes which do not project laterally and whose centres are opposite or slightly behind the anterior ends of S1; eye-ridges weak or absent; inter-ocular cheeks more than half as wide as glabella (about two-thirds as wide as glabella in shale-preserved specimens) at eye-line; occipital spine relatively long; free cheek semicircular with long spine springing from the middle of the lateral margin; thorax with axial nodes and pleural spines, pleural regions about two-thirds as wide as the axis; pygidial outline rounded behind, pleural regions about two-thirds as wide as axis which is composed of about three rings.

Description. The general features of the cranidium are very like those of *S. humilis*. Glabella prominent but commonly flattened in shale-preserved specimens, in which cases the axial furrow may be deepened. S1 oblique backwards, concave, joined across glabella in an even curve; S2 very short or indistinct impressions in the sides of the glabella. Occipital spine long but in many specimens only a tubercle is preserved.

EXPLANATION OF PLATE 78

Sphaerophthalmus species, $\times 6$.

Figs. 1 and 5 are of specimens from the Upper Dolgelly Beds near Dolgelly, Merioneth (Belt Collection); the remainder are from the White Leaved Oak Shales of the Malvern Hills.

Figs. 1–8. *S. major* Lake. 1. Small cranidium showing long occipital spine, BM I 7619 *partim* (see Fig. 5). 2. Lectotype cranidium, GSM 8903. 3. Cranidium showing mould of occipital spine, SM A53115. 4. Cranidium, SM A53088. 5. Cephalon and thorax, paratype, BM I 7619 *partim*. 6, 7. Free cheeks, SM A52564, 52562. 8. Thorax and pygidium, paratype, SM A509.

Figs. 9, 10. *S. cf. alatus* (Boeck), external moulds of cranidium and free cheek, SM A53130.

Figs. 11–15. *S. humilis* (Phillips). 11, 12. Cranidia, SM A53093, GSM 8963. 13. Cranidium from Phillips's Collection, Ox A287a. 14. Free cheek, SM A52546. 15. Thorax and pygidium figured by Lake, GSM 8913.

Photographs by Mr. J. M. Pulsford.



1



2



11



3



4



12



5



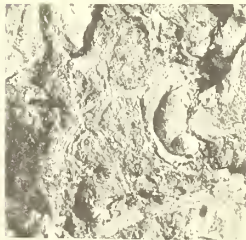
6



7



13



14



9



10

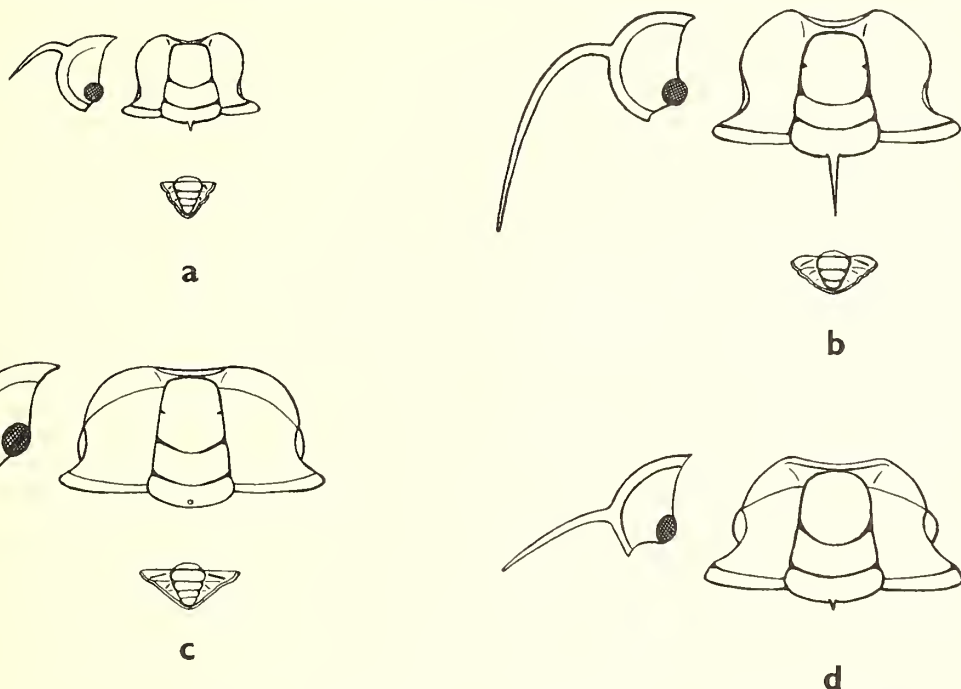


8



15

Anterior border short (sagittally), strongly arched in anterior view but probably only slightly emarginate in dorsal view; in the lectotype it is strongly emarginate and up-turned because compressed. Eye-ridges very weak on both internal and external moulds, moderately oblique. Palpebral lobe narrow, arched up in lateral view, emarginate in dorsal view; centres opposite or just behind the anterior ends of S1. Inter-ocular cheeks about two-thirds of the glabellar width at the eye-line, but probably little more than half in specimens preserved with their full convexity; post-ocular cheeks as wide as to four-fifths the width of the occipital ring, but probably about two-thirds in convex specimens.



TEXT-FIG. 3. Diagrammatic drawings of flattened cranidia, free cheeks and pygidia of *Sphaerophthalmus* species, about $\times 4$. (a) *S. humilis* (Phillips), partly after Westergård. (b) *S. major* Lake (the pygidium is partly conjectural). (c) *S. majusculus* Linnarsson; pygidium, associated cranidium (after Westergård) and doubtfully attributed free cheek (after Henningsmoen). (d) *S. alatus* (Boeck), after Westergård (pygidium unknown).

Free cheek semicircular with a curved spine up to twice as long as the genal field springing from the middle of the lateral margin. Border of about even width. The hemispherical eye is placed far back but distinctly forward of the border-furrow.

The thorax and pygidium have been adequately described by Lake, but it should be noted that the pleural and axial spines are generally not preserved, and that the pygidial flanks may bear more than one pair of furrows.

Comparison with other species (text-fig. 3). Compared with *S. major* *S. humilis* (text-fig. 3a; Pl. 78, figs. 11–15) has narrower fixed cheeks; the inter-ocular cheeks in convex specimens are less than half as wide as the glabella at the eye-line and even when

flattened they are only slightly more than half. The eyes are further back in *S. humilis* and the eye-ridges are consequently more oblique, the occipital and genal spines are shorter, the border of the free cheek tends to widen forwards, the pleural regions of thorax and pygidium are narrower and the pygidium is triangular rather than rounded behind. Measurements made on several specimens from the White Leaved Oak Shales have shown that the width of the inter-ocular cheeks of *S. humilis* is 0.53 or less of the width of the glabella, whereas that of *S. major* is 0.63 or more.

S. alatus (text-fig. 3d; cf. Pl. 78, figs. 9, 10) resembles *S. major* in having the palpebral lobes opposite S1 and has fixed cheeks of comparable width, but it differs in having palpebral lobes that project laterally and are joined to the glabella by distinct eye-ridges; the anterior ends of S1 are further forward in relation to the length of the cephalic axis in *S. alatus* than *S. major*, and the palpebral lobes are correspondingly further forward on the cranium. In *S. alatus* the anterior part of the fixed cheeks narrows forwards; the occipital spine is shorter than that of *S. major* and the cheek spine is set further back; the posterior part of the margin of the free cheek is nearly straight, whereas in *S. major* it is curved.

S. majusculus (text-fig. 3c) has wider fixed cheeks than *S. major*, distinct eye-ridges, palpebral lobes that project slightly laterally, and a node in place of the occipital spine. The free cheek tentatively assigned to the species by Henningsmoen (1957, p. 219) has a shorter spine set further back than that of *S. major*. The pygidium of *S. majusculus* is relatively wider than that of *S. major* and is triangular rather than rounded behind.

Measurements in mm.

	GSM 8903 (lectotype)	SM A53088
Length of cranium	4.2	c. 3.4
Width of cranium at eyes	5.0	4.1
Width of cranium posteriorly	6.6	5.6
Length of cephalic axis	3.5	2.9
Width of cephalic axis	2.6	1.9

Sphaerophthalmus major probably reached a total length of about 10 mm.

Occurrence. *Sphaerophthalmus major* is found within the Zone of *Peltura scarabaeoides* in England, Wales, Sweden, possibly in Nova Scotia (Canada), and apparently also in Norway; such evidence as there is suggests that it occurs in the Subzone of *Ctenopyge linnarssoni*. In discussing these occurrences reference is made to Henningsmoen's (1957, p. 39) subdivisions of the *P. scarabaeoides* Zone:

<i>P. scarabaeoides</i> Zone	{	<i>Peltura paradoxa</i> Subzone
		<i>Parabolina lobata</i> Subzone
		<i>Ctenopyge linnarssoni</i> Subzone
		<i>Ctenopyge bisulcata</i> Subzone

In Scandinavia *Ctenopyge bisulcata* (Phillips) and *C. linnarssoni* Westergård are known only from their own subzones, whereas *C. pecten* (Salter), *P. scarabaeoides* (Wahlenberg), and *Sphaerophthalmus humilis* (Phillips) occur in both subzones.

England. The lectotype of *S. major* is from the White Leaved Oak Shales of the Malvern Hills. The detailed stratigraphy of these Shales is unknown and though the presence of

the *C. bisulcata* Subzone is indicated by the association on single pieces of shale of *C. bisulcata*, *C. pecten*, *S. humilis*, and *P. scarabaeoides*, the presence of the *C. linnarssoni* Subzone is not proved. *S. major* has not been seen in association with undoubted fragments of *C. bisulcata*, but occurs with *C. pecten* and fragments of a *Ctenopyge* species recalling *C. bisulcata*, *C. linnarssoni*, or *C. falcifera* Lake.

In the Geological Survey Merevale No. 1 Borehole, which penetrated the Monks Park Shales (Upper Stockingford Shales) in Warwickshire (Kellaway 1966), poorly preserved specimens of *S. major* were collected at depths of 190 ft. 6 in. and 193 ft. 0 in., from horizons slightly higher than those yielding *S. humilis* and *C. bisulcata* (depths of 205 ft. 6 in. and 206 ft. 6 in.).

Wales. One paratype of *S. major* is from the Upper Dolgelly Beds of the Dolgelly area in North Wales; the precise locality and zonal position are unknown. Lake records *S. major* from Moel Gron, near Dolgelly.

Sweden. A block of Upper Cambrian bituminous limestone in the Sedgwick Museum, collected by Mr. S. C. A. Holmes from Vilske-Klefua, Västergötland, Sweden (SM A56378-87), carries an association of *S. major* with *Ctenopyge fletcheri* (Matthew) and *Peltura scarabaeoides westergaardi* Henningsmoen, suggesting a horizon near the junction of the Subzones of *C. linnarssoni* and *Parabolina lobata* (see Henningsmoen 1957, p. 39).

Norway. Henningsmoen (1957, pl. 22, figs. 7, 15) illustrated two cranidia from the Subzone of *C. linnarssoni* at Viul, Ringerike, Norway, under the name of *Sphaerophthalmus humilis*; the fixed cheeks are too wide and the occipital spine rather too large for that species and they are more probably cranidia of *S. major*.

Nova Scotia. Hutchinson (1952, p. 90) records *S. major* from the upper part of the MacNiel formation (*Peltura* Zone), and figures two specimens on his plate 4; one (fig. 16) is probably *C. fletcheri* incorrectly identified as *S. major* but the other (fig. 17) may be *S. major* (Henningsmoen 1957, pp. 205, 218).

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A. W. A. RUSHTON
Institute of Geological Sciences
Exhibition Road
London, S.W. 7

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PROBABLE ANGIOSPERM POLLEN FROM BRITISH BARREMIAN TO ALBIAN STRATA

by ELIZABETH M. KEMP

ABSTRACT. Two species of the genus *Clavatipollenites* Couper are described. One is a redescription of the type species, *Clavatipollenites hughesii*, from the Upper Barremian part of the Wealden Series. The other, *Clavatipollenites rotundus*, is a new species from the Middle Albian Lower Gault. Three species of tricolpate angiospermous grains are described. Only one of these, *Tricolpites albiensis*, from the Upper Albian, occurs in sufficient quantity to be formally named as a new species. These forms constitute the earliest record of recognizable angiosperm grains from England.

DURING an investigation into the spore and pollen assemblages of the marine Lower Greensand and Gault of southern England, several pollen species were recovered which are of particular botanical and stratigraphical interest. Two of these are monosulcate pollens referable to the genus *Clavatipollenites* Couper; the others are tricolpate angiospermous forms, the earliest undoubted pollen of this group from England. Of these last forms, only one was recovered in sufficient quantity to permit formal designation as a new species. The monosulcate pollens described here are of interest in that they possess some angiosperm characters and their appearance slightly predates that of grains of undoubted angiospermous affinity.

Acknowledgements. Research facilities in the Department of Geology, Sedgwick Museum, Cambridge, were made available by Professor O. M. B. Bulman. Mr. N. F. Hughes took a constant interest in the course of this work and provided the sample from the Kingsclere Borehole. Financial assistance was provided by a British Commonwealth Scholarship from 1963 to 1966.

LOCATION AND STRATIGRAPHY OF SAMPLES

The samples yielding the type material of the new species described here are part of a more extensive collection of Lower Greensand, Gault and Upper Greensand. The systematic and stratigraphic palynology of these sediments has been investigated in detail for an unpublished thesis. The sediments are of Aptian and Albian age, with a rich fauna which permits their subdivision in terms of ammonite zones.

The Lower Greensand samples have been collected chiefly from the Isle of Wight, with minor sampling in the Weald and in the northern sedimentary basin near Leighton Buzzard. The Gault and Upper Greensand have been collected over a wider geographic area, extending from near Leighton Buzzard, through sections in the northern Weald to the Isle of Wight and the Dorset coast in the south and south-west. In addition, the sample from 475 ft. in the Kingsclere Borehole, previously studied by Couper (1958), has been re-examined as it provided the type material of the species *Clavatipollenites hughesii*. This species persists into younger strata. The type sample comes from the Wealden, and is probably of Upper Barremian age.

More detailed references to the samples used in this study and to the sections from which they were collected are given below:

Sample F154—Calcareous pale yellowish-grey clay with shell fragments. Gault at Ford Place, Wrotham (Nat. Grid. reference 51/636591). Bed 20, near base; *niobe* Subzone of the *dentatus* Zone; Middle Albian. The detailed stratigraphy of this clay pit is given by Milbourne (1963), who subdivided the section into 82 beds on the basis of lithology.

Sample K475—Medium-grey siltstone with small dark patches, possibly plant fragments. Wealden Series, 475 ft. in the D'Arcy Exploration Company's Kingsclere No. 1 Borehole; probably Upper Barremian. Further details of the palynology and stratigraphic position of this sample are given by Hughes (1958) and Couper (1958).

Sample F312—Calcareous friable pale yellowish-green silty sandstone. Upper Greensand, west side of Lulworth Cove, Dorset (Nat. Grid reference 30/825799). 18 ft. beneath the base of the *Exogyra* Rock, which underlies a series of stone bands at the top of the Upper Greensand and serves as a convenient local marker (Wright, in Arkell 1947). Beds above the *Exogyra* Rock can be referred to the *dispar* Zone. The zonal position of the beds below is less certain, but they are probably of Upper Albian age.

Sample F270—Grey and cream mottled sandstone with ferruginous pebbles and patchy iron staining. Munday's Hill pit, Leighton Buzzard (Nat. Grid reference 42/930265). 6 in. beneath base of Carstone Breccia in the upper part of the Woburn Sands. The precise age of the sample is unknown. The Carstone Breccia is partly of Lower Albian age; the sample in question comes probably from the Lower Albian.

Location of type material. Rock samples, strew slides and individual mounts made from preparations are lodged in the Sedgwick Museum, Cambridge. Slides are deposited in the Palynology Collection of that museum. Formally named species are based on examination of 100 specimens in each case, and all of these are available for restudy. The co-ordinates quoted are those of the Leitz Dialux microscope Serial No. 526724 in the Sedgwick Museum.

Preparation procedures. Spore assemblages were extracted by solution of silicates in cold hydrofluoric acid following the removal of carbonates, where necessary, with 10–15 per cent. HCl. Residues were oxidized in Schulze solution, two short periods of oxidation usually being used. The total oxidation time did not in any case exceed twenty minutes. Residues were briefly cleared in less than 1 per cent. NH_4OH and the microfossils separated from the remaining mineral debris by centrifuging in zinc bromide solution.

SYSTEMATIC PALYNOLOGY

Anteturma POLLENITES Potonié 1931

Turma PLICATES Naumova 1939 emend. Potonié 1960

Subturma MONOCOLPATES Iversen and Troels-Smith 1950

Genus CLAVATIPOLLENITES Couper 1958

1958 *Clavatipollenites* Couper, p. 159.

1961 *Retimonocolpites* Pierce, p. 47.

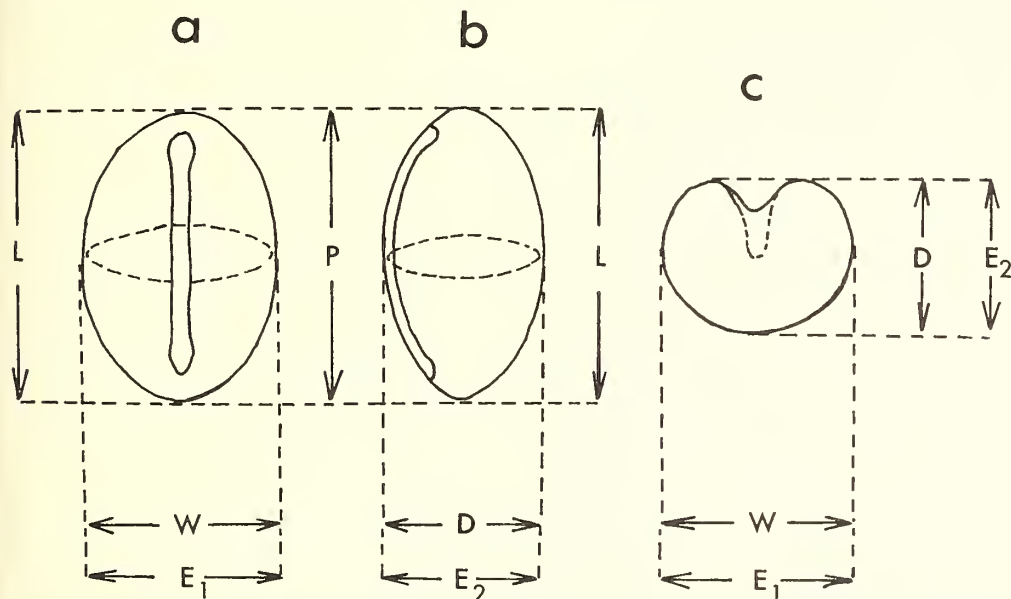
Type species. *Clavatipollenites hughesii* Couper 1958, p. 159, pl. 31, figs. 19–22.

Diagnosis. As given by Couper (1958).

Remarks. On a morphological basis *Clavatipollenites* resembles *Liliacidites* Couper (1953, p. 56) which was proposed to incorporate monosulcate grains of reticulate exine pattern, or, more precisely, 'for the reception of fossil pollens of liliaceous affinities that

cannot be more accurately placed'. The species originally referred to *Liliacidites* formed part of an Upper Cretaceous and Tertiary complex which had a large component of grains of unquestionably angiospermous origin. It would seem that the retention of a separate genus is valuable for Lower and lower Upper Cretaceous forms the affinity of which is in question.

Species from several widely separated localities have been referred to *Clavatipollenites*. Not all of these, however, conform to the diagnosis of the genus. Pocock (1962, p. 74,



TEXT-FIG. 1. Grain orientation in *Clavatipollenites*. L = length, W = width, D = depth. Designations P, E₁, and E₂ correspond with those of Couper (1958) for describing monosulcate and tricolpate pollens. Orientation: a, polar view; b, equatorial longitudinal view; c, equatorial transverse view.

pl. 12, figs. 190–2) described a large form which he named *Clavatipollenites couperi*, from the Upper Jurassic–Neocomian Vanguard Formation of western Canada. The specimens he figured do not show the presence of a tectate exine convincingly, and the species may perhaps be more accurately referred to *Monosulcites* or *Ginkgocycadophytus*. Helal (1965, pl. 17, fig. 19; 1966, pl. 34, figs. 54, 55) recorded both *C. couperi* and *C. hughesii* from subsurface Jurassic sediments in the Western Desert, Egypt. Both of the grains figured by this author appear to be distinctly three-furrowed, suggesting *Eucommiidites* rather than *Clavatipollenites*.

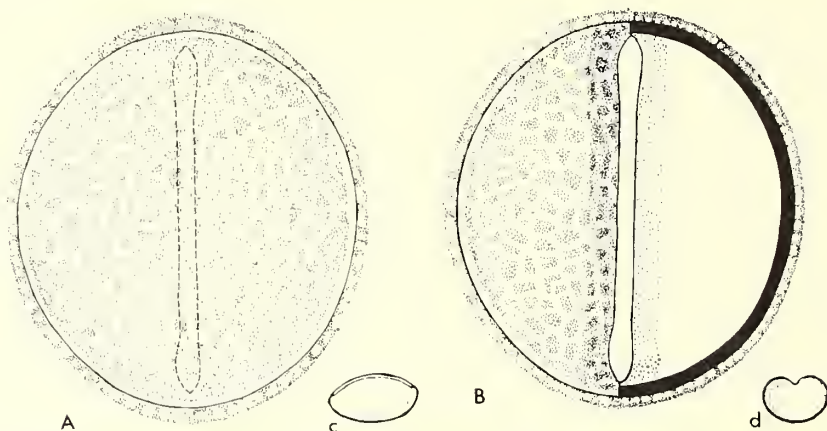
The type species, *C. hughesii*, has been recorded by Brenner (1963) together with a smaller form which he designated *C. minutus*, from Potomac Group sediments in Maryland. Von der Brelie (1965, p. 151, pl. 13, figs. 6–8) found *C. hughesii* in sediments of probable Aptian–Albian age in Germany. Archangelsky and Gamarro (1967) reported the presence of the species in assemblages of probable Barremian age in southern Argentina.

Pierce (1961, p. 47, pl. 3, fig. 87) described a monosulcate pollen from Cenomanian clays and lignites in Minnesota. This species, which he named *Retimonocolpites dividius*,

Pierce designated as type species of the genus *Retimonocolpites*. This genus is regarded as synonymous with *Clavatipollenites* on the basis of Pierce's definition.

Both the type species, *C. hughesii*, and a new species, *C. rotundus*, were recorded from samples investigated during the present study. The expanded description of *C. hughesii* given below is based on re-examination of specimens from Couper's type sample.

The terminology of the grain dimensions and orientations used in the descriptions is shown in text-fig. 1. Comparisons of the size and shape of grains assigned to the two species are shown in the scatter diagram text-fig. 4, histograms of size frequency distributions in text-fig. 5.



TEXT-FIG. 2. Diagrammatic representation of *Clavatipollenites rotundus* sp. nov. Large figures, $\times 2,000$. A, proximal face, LO pattern, position of sulcus dotted. B, distal face, left-hand side showing reticulum, right-hand side showing exine stratification in section. Dark zone adjacent to the sulcus is stippled. C, equatorial longitudinal view. D, equatorial transverse view.

Clavatipollenites rotundus sp. nov.

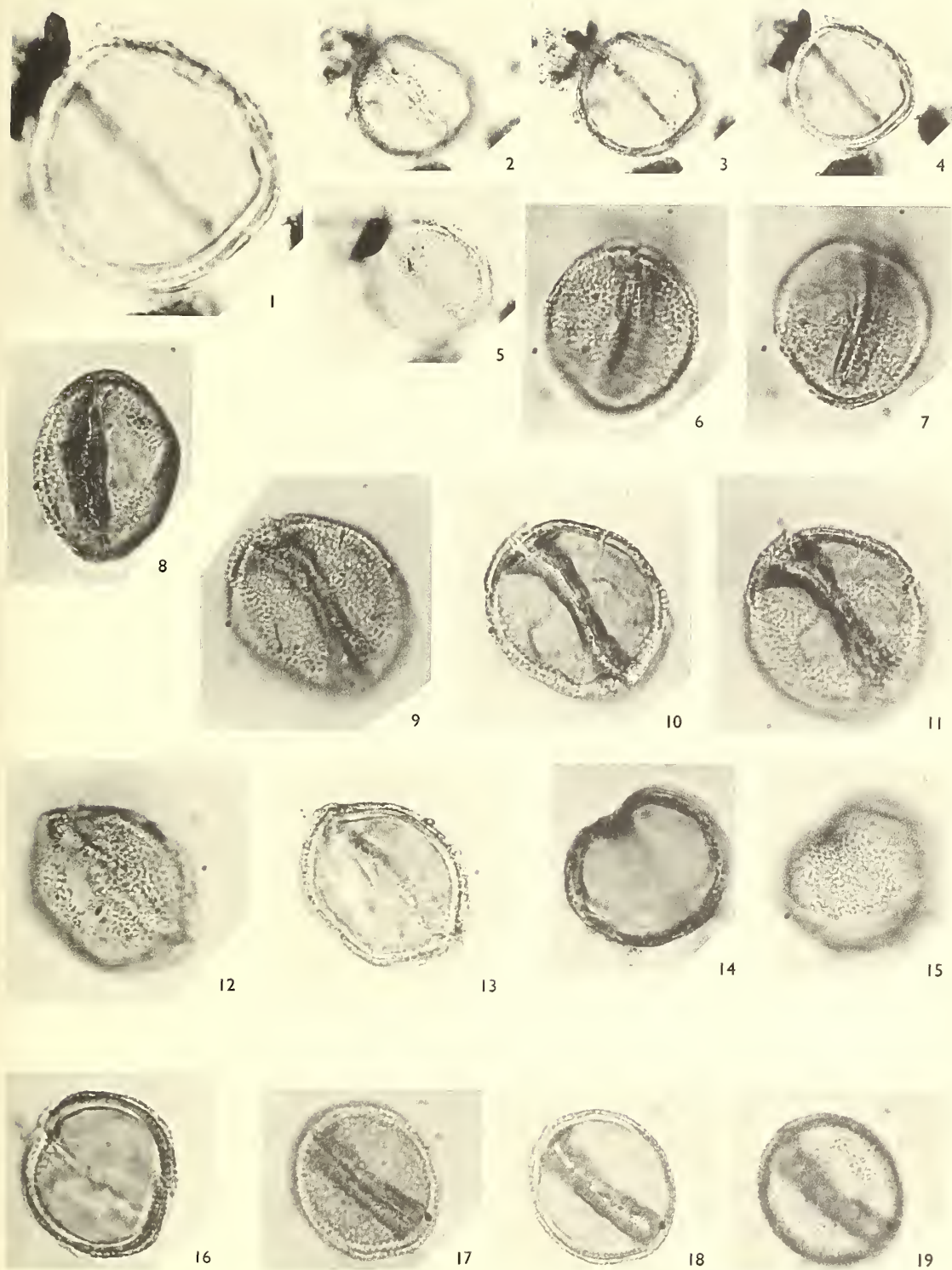
Plate 79, figs. 1-19; Plate 80, figs. 1-8; text-fig. 2

Diagnosis. Monosulcate pollen grains of subcircular to elliptical outline, with a distinctly tectate exine. The sulcus is conspicuous, round-ended, and bordered by thicken-

EXPLANATION OF PLATE 79

All figures at magnification $\times 1,000$ unless otherwise stated.

Figs. 1-19. *Clavatipollenites rotundus* sp. nov. All specimens from sample F154, *niobe* Subzone of the *dentatus* Zone, Lower Gault at Ford Place, Wrotham. 1-5, F154/2; 35.0, 92.7. 1, Median focus showing tectate exine in section at equator ($\times 2,000$). 2, High focus on sulcus. 3, 4, Deeper foci. 5, Proximal focus on reticulum with sexine partly detached. 6, 7, F154/11; 27.0, 108.2; grain obliquely compressed. 6, Deep focus. 7, High focus showing end of sulcus and darkened zone. 8, F154/Separate 15, 40.0, 97.6; grain showing pronounced infolding associated with sulcus. 9-11, F154/Separate 1; 38.3, 99.2. 9, Proximal focus showing reticulum. 10, Median focus on sulcus and associated structure. 11, Distal focus. 12, 13, F154/10; 34.2, 90.2. 12, High focus on proximal face, sexine partly removed. 13, Equatorial focus. 14, 15, F154/12; 35.8, 89.8. 14, Median focus of specimen in end-on view. 15, High focus on reticulum. 16, F154/Separate 8; 39.0, 98.1; median focus showing folding adjacent to sulcus. 17-19, F154/Separate 9; 39.2, 98.5; Holotype. 17, High focus on distal face. 18, Median focus on sulcus with exine stratification distinct at equator. 19, Proximal focus.



ings or infoldings of the nexine. The reticulate pattern of the sexine is formed from the fused tips of bacula; the mesh diameter is from 0.7 to $2.0\ \mu$. The mean grain width lies in the range 22 – $27\ \mu$, mean grain length 25 – $30\ \mu$. Sexine shows a tendency to separate from nexine.

Holotype. Sample F154, separate mount 9; 39.2 , 98.5 . Plate 79, figs. 17–19. Lower Gault, Ford Place, Wrotham; Middle Albian. Grain orientated with sulcus uppermost, extending full length of grain, bordered by darkened zone 2.4 – $2.5\ \mu$ wide on either side. Sulcus slightly expanded and rounded at extremities. Nexine $0.8\ \mu$ thick, sexine $1.2\ \mu$. Length $\times$ width $26 \times 25\ \mu$.

Dimensions. (Measured on 100 specimens from Sample F154; see text-fig. 5.) Grain length $20(27)32\ \mu$, grain width $18(25)31\ \mu$, grain depth $17(22)28\ \mu$.

Orientation. (For grain positions see text-fig. 1.) Grains in position *a*—68 per cent., position *b*—7 per cent., position *c*—25 per cent.

Description. The original grain shape, as deduced from measurements and from grain orientations appears to have been subspheroidal to oblate spheroidal. The ratio grain length to grain width is shown in the scatter diagram text-fig. 4.

The sulcus extends for almost the full length of the grain and is parallel-sided throughout most of its length, but frequently shows slight expansion at the extremities. The ends are usually rounded. Most specimens show a darkened zone 1.5 – $2.0\ \mu$ wide on either side of the sulcus throughout its length. This either represents a thickening of the nexine adjacent to the sulcus or a doubling of this layer caused by infolding consequent on rupture of the grain along the sulcus. Optical sections of grains (text-fig. 3) suggest that the last interpretation is more likely to be correct. Some specimens, for example, that illustrated in text-fig. 3*b*, show a small gap in the thickened nexine layer adjacent to the sulcus, suggestive of breakage during infolding and compression. These sections also demonstrate that the sexine is not involved in the infolding.

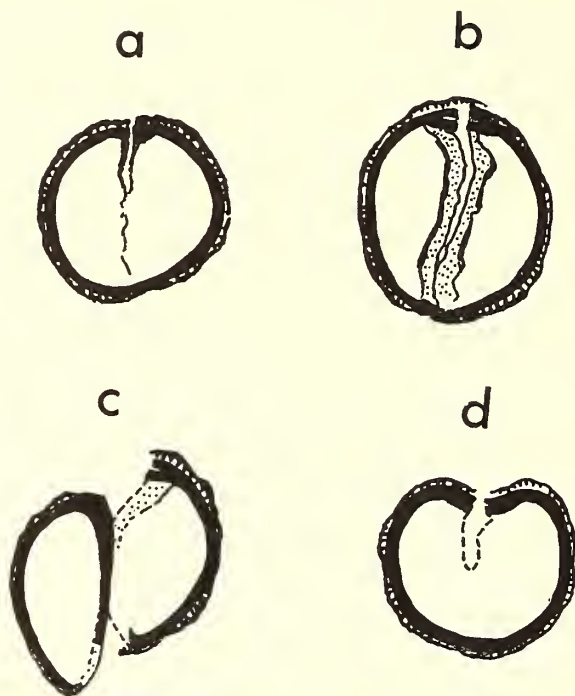
The stratification of the exine is distinct. The nexine is 0.8 – $1.8\ \mu$ thick. The bacula arising from this layer expand and coalesce at their tips to form the reticulum of the ectosexine. The meshes of the reticulum are irregularly polygonal, separated by muri 0.3 – $0.5\ \mu$ wide, which are formed from single rows of fused bacula. The meshes are generally of uniform size over the entire grain surface. The sexine characteristically separates from the nexine; separation is usually more extreme at the grain ends. Some grains were observed in which the sexine had been entirely removed.

Remarks. *Clavatipollenites rotundus* appears similar to Pierce's species *Retimonocolpites dividuus*, although the single illustration given by Pierce (1961, pl. 3, fig. 87) makes comparison difficult. Pierce does, however, mention the tendency for the exine layers to separate. Brenner (1963) recombined Pierce's species with *Liliacidites*, with little descriptive comment. The specimens from the Patapsco Formation show some evidence of infolding adjacent to the sulcus but not to the degree seen in the English forms. The American species appears less spherical and thinner and consequently tends to fold more readily than its English counterpart.

Distribution. In England *C. rotundus* is confined to Albian sediments. Its earliest recorded appearance is in Sample F270, which is probably of Lower Albian age. This occurrence is the only one observed beneath the base of the Gault. The species was noted in greatest abundance in the vicinity of the *niobe*

Subzone at Wrotham and at Folkestone, although it persists throughout the Albian. These concentrations, which do not in any case exceed 5 per cent. of the total spore and pollen content, may be due to a facies factor as they are associated with a rich benthonic fauna and ferruginous bands.

The distribution in time of *C. dividius* is similarly restricted in America. Brenner (1963) records the species as being confined to the Patapsco Formation (Albian).



TEXT-FIG. 3. Optical sections of specimens of *Clavatipollenites rotundus* sp. nov., drawn from photographs to show the structure associated with the sulcus. All $\times 1,000$. Nexine shown solid black. *a*, F154/Separate 8; 39.0, 98.1; nexine appears as thickening adjacent to sulcus. *b*, F154/Separate 1; 38.3, 99.2; optical section of grain in equatorial view. Slight obliquity causes sulcus to appear in section at top of drawing. Sexine is detached, not involved in infolding; the nexine adjacent to the sulcus appears split. Darkened zone next to the remainder of sulcus shown stippled. *c*, F154/10; 36.6, 106.0; split grain showing a similar structure to *b*. *d*, F154/2; 32.0, 100.1; grain in end-on view.

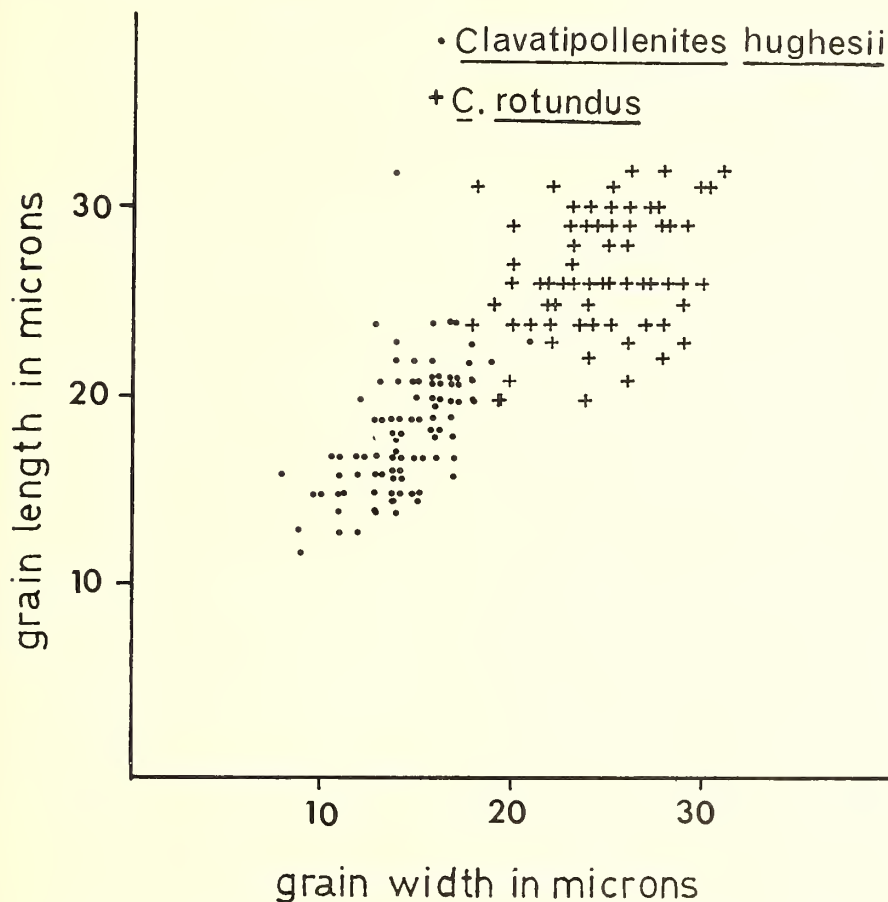
Clavatipollenites hughesii Couper emend.

Plate 80, figs. 9-19

Remarks. Couper (1958) gave no separate diagnosis for *C. hughesii*, so his description has been emended slightly and is here restated as a diagnosis.

Emended diagnosis. Monosulcate pollen grain, sulcus extending full length of grain, gaping in its central region and tapering slightly towards extremities. Equatorial outline elliptical to subcircular. Exine consisting of an inner unsculptured nexine $0.5-1.0 \mu$ thick

and a sexine formed of baculate projections approximately 1.0μ long, which either remain discrete or fuse at their tips to form a microreticulum. Lumina of reticulum irregularly polygonal, $1.0\text{--}2.0\mu$ in diameter.

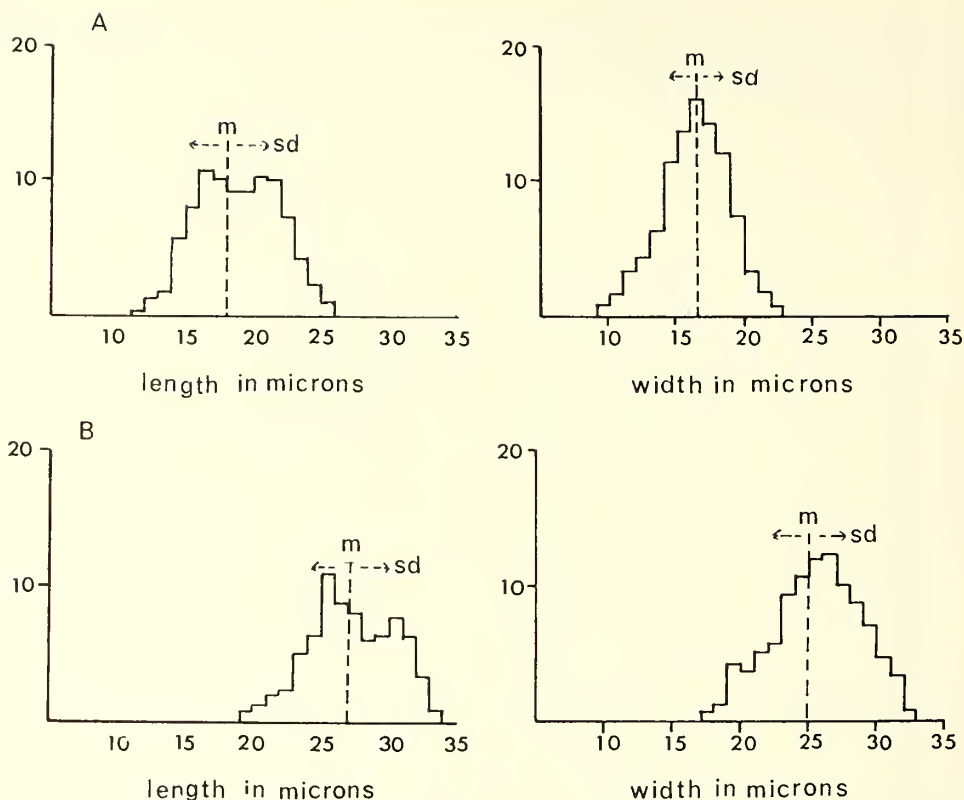


TEXT-FIG. 4. Scatter diagram showing differences of shape and size between *Clavatipollenites hughesii* Couper and *C. rotundus* sp. nov. Based on 100 specimens from each of the type samples, K475 Kingsclere Borehole, and F154, Ford Place, Wrotham.

Holotype. Couper (1958, pl. 31, figs. 21, 22). Slide C128/9, specimen K5087; 35.8, 114.2. Kingsclere Borehole at 475 ft. Grain orientated with sulcus uppermost. Length $\times$ width $28.0 \times 17.5\mu$.

Dimensions. (Measured on 100 specimens from the type sample.) Histograms of size frequency distributions are shown in text-fig. 5. Grain length 12(18)30 μ , width 8(16)19 μ , depth 12(13)17 μ .

Description. The outline of the grains is variable, ranging from almost circular to strongly elliptical. Margin of sulcus often ragged. The sulcus is frequently indistinct, or represented as an indeterminate tear in the exine. The grains are often folded with the long axes of the folds parallel to the sulcus.



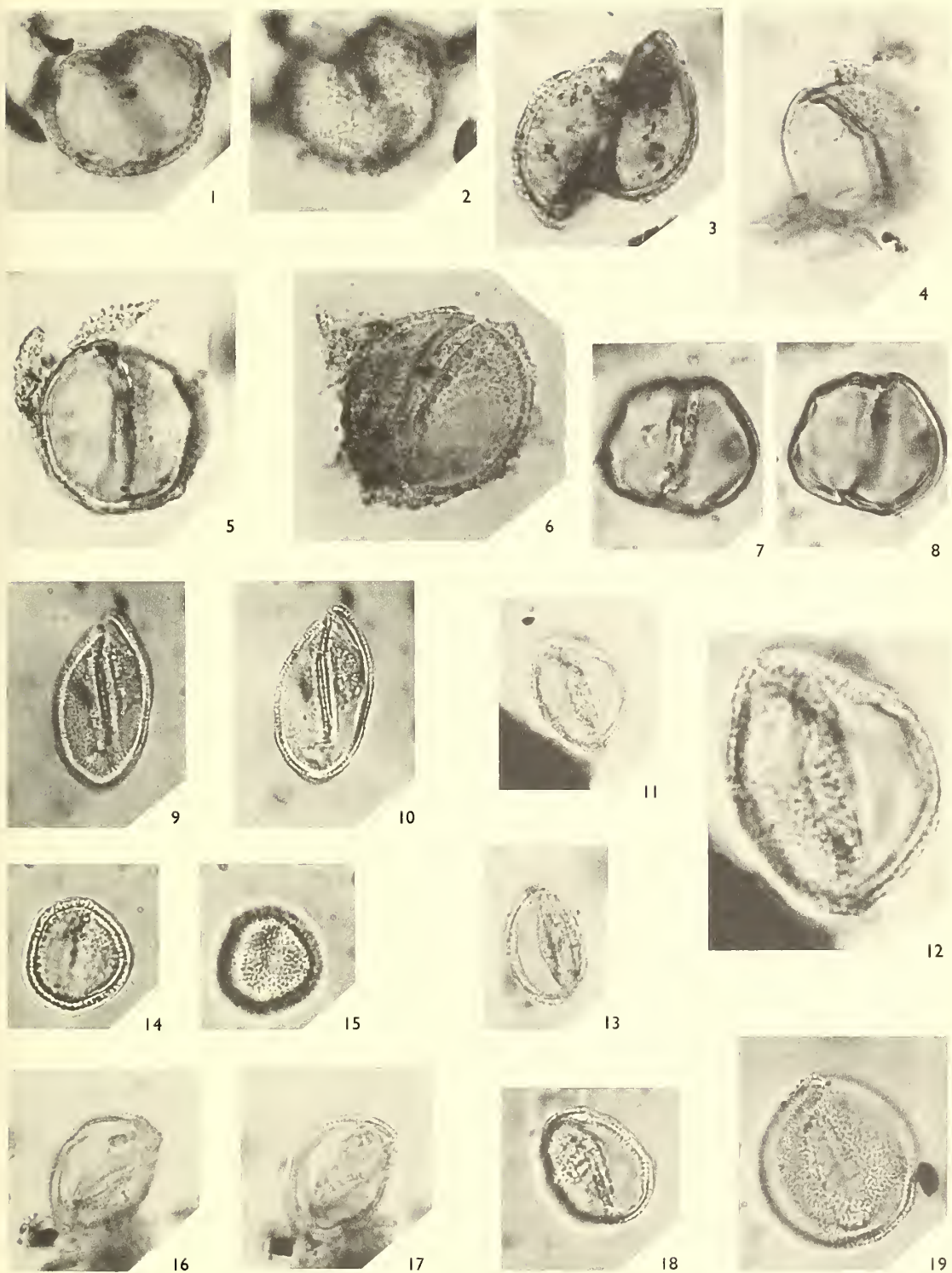
TEXT-FIG. 5. Histograms showing frequency distribution of grain lengths and widths in A, *Clavatipollenites hughesii* and B, *C. rotundus* sp. nov. Graphs smoothed using a three-point moving average.

EXPLANATION OF PLATE 80

All figures at magnification $\times 1,000$, unless otherwise stated.

Figs. 1–8. *Clavatipollenites rotundus* sp. nov. All specimens are from sample F154, *niobe* Subzone of the *dentatus* Zone. Lower Gault at Ford Place, Wrotham. 1, 2, F154/2; 32.2, 100.1. 1, Median focus, end-on view. 2, High focus on reticulum and extremity of sulcus. 3, F154/10; 36.6, 106.0; specimen split along sulcus, infolded zone adjacent to sulcus visible. 4, F154/7; 27.3, 91.8; sexine has been partly removed. 5, F154/7; 26.6, 101.1; sexine partly removed. 6, F154/Separate 4; 39.9, 97.3; part of grain in equatorial focus, sexine loose. 7, 8, F154/4; 39.9, 94.2; specimen from which sexine has been completely lost. 7, High focus showing dark zone adjacent to sulcus. 8, Median focus.

Figs. 9–19. *Clavatipollenites hughesii* Couper. 9, 10, Slide BP174A (IX); 60.0, 104.4 (N. F. Hughes Coll. No.). 9, High focus showing bacula in surface view. 10, Deep focus showing sulcus and exine stratification. Kingsclere Borehole at 475 ft. 11, 12, F154/1; 26.7, 107.0. 11, Median focus showing sulcus and exine stratification. 12, The same at $\times 2,000$. 13, F154/5; 28.1, 92.5; median focus, sulcus and exine stratification shown. Ford Place, Wrotham; Middle Albian. 14, 15, K475/2; 23.2, 101.1. 14, Equatorial focus showing bacula in section. 15, High focus showing surface pattern; Kingsclere Borehole at 475 ft. 16, 17, F154/2; 54.2, 92.8. 16, High focus showing sulcus. 17, Equatorial focus showing exine stratification. Ford Place, Wrotham; Middle Albian. 18, F154/5; 23.9, 90.0; median focus on compressed grain. Ford Place, Wrotham. 19, F099/1; 55.0, 104.0; high focus on grain with irregular, gaping sulcus. Compton Bay, Isle of Wight; Middle Albian.



Remarks and comparison. The dimensions quoted are smaller than those quoted by Couper and cover the range of the species *C. minutus* Brenner, which may be conspecific with *C. hughesii*. The histograms of size-frequency distribution do not suggest any ready subdivision of the species on a size basis. The larger size quoted by Couper may be due to some extent to the maceration technique employed. The specimens measured in the present study were isolated from a fresh preparation of the type material which was subjected to only fifteen minutes oxidation time in contrast to the minimum of six hours quoted by Couper.

C. hughesii and *C. rotundus* are readily separable on the basis of their size ranges and on the shape of the grains. Text-fig. 4 illustrates these differences. In *C. hughesii* most grains are longer than they are wide. *C. rotundus* shows greater variation in the ratio length to width, with slightly less than half the grains being wider than long.

In *C. rotundus* the sulcus is a conspicuous feature, rounded at the extremities and modified by probable infolding at its margins. In some of the grains referred to *C. hughesii* the sulcus is barely discernible. Where visible it is a ragged opening, tapering towards its extremities and lacking the marginal rigidity of that in *C. rotundus*.

A third feature which separates the species is the degree of development of the ectosexinous reticulum. The bacula of the sexine in *C. rotundus* almost invariably unite at their tips to form the muri of an unbroken reticulum; in *C. hughesii* they often remain discrete or unite in short broken rows only to form an imperfect reticulum.

Distribution. The first occurrence of *Clavatipollenites hughesii* in the Barremian has been recorded by Hughes (1958). In about half the Lower Greensand samples examined during the present study it occurred in concentrations somewhat less than 1 per cent. of the total spore and pollen assemblages. It persists throughout the Gault to Upper Albian horizons, although with a much lower sample frequency. The highest recorded concentrations occur near the top of the Atherfield Clay (up to 10 per cent.).

Affinity of Clavatipollenites. The feature of greatest botanical interest in fossil pollen of the *Clavatipollenites* type is the presence of a tectate exine. It was this feature which led Couper (1958) to suggest an angiospermous origin. He compared *C. hughesii* to grains of the extant dicotyledon *Ascarina lucida* and also drew attention to structural similarities of pollen of certain members of the Liliaceae. *C. hughesii* represents, to present knowledge, the earliest record of this type of exine organization, although it may be argued that parallels exist among disaccate pollens. *Clavatipollenites* first appears in spore and pollen assemblages which lack any other obvious angiosperm elements, a fact which justifies close attention being paid to the genus.

In spite of the angiospermous character of some of the features of *Clavatipollenites* it still remains possible that the grains were produced by a member of some extinct gymnosperm group. The over-all shape of the grains resembles that of both living and fossil cycadophyte pollen. The form of the sulcus, particularly where this is rounded at its extremities, is closer to that of living cycad pollens than to most angiosperm pollen.

The orientation of the grains observed in *C. rotundus* shows a pronounced tendency towards proximo-distal compression. This suggests that the proximo-distal axis E_2 (designations as used by Couper, 1958, pp. 162-3) is shorter than the other equatorial axis E_1 . This observation indicates a similarity of shape to that of the grains of *Androstrobis manis* and *Ginkgo huttoni* as these were analysed and presented by Couper.

It is apparent that species referred to *Clavatipollenites* are characterized by features suggesting the possibility of either angiosperm or gymnosperm parentage. All discussion of affinity is, however, purely speculative, and the problem can only be resolved by discovery of the grains in association with other reproductive structures.

Subturma TRIPTYCHA Naumova 1939

Remarks. Potonié (1960, p. 92) has treated Naumova's category as a subturma, although it was originally intended as a broadly defined form genus. Potonié has remarked that the category is used as Tricolpites in Erdtman's (1947) sense; i.e. as a broad supra-generic category incorporating tricolpate grains of indeterminate affinity.

Genus TRICOLPITES Cookson ex Couper 1953

Type species. *Tricolpites reticulatus* Cookson 1947, p. 134, pl. 15, fig. 45. (Subsequent designation, Couper 1953.)

Remarks. The use of a broadly circumscribed form genus for early tricolpate pollens is considered adequate and non-committal. The diagnosis of *Tricolpites* given by Couper (1953, p. 61) is as follows: 'Grains free, anisopolar, tricolpate. Exine variable in thickness and sculpture. Size variable.'

Other authors dealing with early tricolpate pollens have referred them to *Tricolpopollenites* Thomson and Pflug (see Groot and Penny 1960, Brenner 1963). The diagnosis of this form genus implies the presence of some form of germinal structure in the equatorial region of the colpi, although it is not precise as to the form of this feature; 'Exitus nur als meridionale Colpen ausgebildet' (Thomson and Pflug 1953, p. 95).

Pierce (1961) referred Cenomanian tricolpate grains to *Retitricolpites* van der Hammen, but this genus is not regarded as valid under the International Rules of Nomenclature since the type of *R. vulgaris*, the type species, is a grain of the extant species *Neea macrophylla*.

Tricolpites albiensis sp. nov.

Plate 81, figs. 1–22, text-fig. 6

Diagnosis. Small (less than 20 μ diameter) tricolpate pollen grains in which the ratio of polar to equatorial diameter lies between 2:1 and 1:1. The bacula of the sexine form an imperfect microreticulum. The total exine thickness is around 1.0 μ .

Holotype. Sample F312/4; 46.8, 90.0. Plate 81, figs. 2–4. From 18 ft. below the base of the *Exogyra* Rock, Upper Greensand, Lulworth Cove, Dorset. Probably Upper Albian, zonal position uncertain. Grain in obliquely polar orientation, with three colpi almost meeting at pole. Grain diameters 16 $\times$ 17 μ . Exine slightly less than 1 μ thick, microreticulate.

Dimensions. Equatorial diameter 7.0(11.4)14.5 μ , polar diameter 10.5(13.5)17.5 μ , ratio of polar to equatorial diameter 1.0(1.35)1.65 (based on measurement of 100 specimens from the type sample).

Orientation. Grains in polar view—73 per cent., equatorial view—19 per cent., oblique view—8 per cent.

Description. Grains are tricolpate, trilobate and radially symmetrical in polar view, oval in equatorial view. The colpi are narrow and the acolpia small in relation to the rest of

the grain; rare grains are almost syncolpate. The margins of the colpi are slightly ragged. The sexine and nexine are of approximately equal thickness. Diameter of meshes of microreticulum $0.3\text{--}0.4\ \mu$.

Comparison. In its general form and size *Tricolpites albiensis* resembles *Tricolpopollenites micromunus* Groot and Penny. The original description of the species was brief, so close comparisons are difficult. *T. micromunus*, however, was described as having a coarsely reticulate exine, which justifies the separation of the English species from it. Brenner (1963, p. 93, pl. 39, fig. 7; pl. 40, fig. 1) gave a fuller description of specimens of *T. micromunus* from the Patapsco Formation, for which he quoted a mean polar diameter of $16\ \mu$, and an equatorial one of $13\ \mu$, which indicates that the American species is slightly larger.

It is possible that the species *Tricolpites minutus* Brenner is conspecific with *T. albiensis* although it appears to be slightly smaller and more spherical than the last species.

Affinity. Speculation as to the affinity of dispersed angiospermous grains of the generalized form of *Tricolpites* cannot be meaningful. Brenner (1963) compared the pollen of the extant species *Tetracentron sinense* to the dispersed species *Tricolpopollenites micromunus*. Similar small tricolpate grains occur in the families Trochodendraceae, Ranunculaceae, Salicaceae, etc.

Distribution. No specimens of *T. albiensis* have been recorded from the Lower Greensand. Rare specimens have been recovered from the Gault (Middle and Upper Albian). In the type locality, the Upper Greensand at Lulworth Cove, the species represented 15 per cent. of the total spore and pollen assemblage.

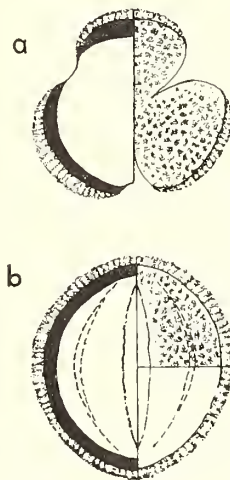
Tricolpites sp. 1

Plate 81, figs. 25, 26

Description. Grains tricolpate, oval in equatorial view, polar views not observed. Colpi distinct, open to a width of $2\text{--}3\ \mu$ in their equatorial regions and acutely pointed at their extremities. A slight thickening of the exine is visible at the margins of the colpi. The ectosexine forms a reticulum in which the meshes are irregular in shape, $1\text{--}3\ \mu$ in diameter. The sexine tends to detach and stand away from the grain in compressed specimens.

Dimensions. Polar diameter $21\text{--}23\ \mu$, equatorial diameter $18\text{--}21\ \mu$ (3 specimens only).

Remarks and comparisons. This grain does not resemble any previously described Cretaceous form, but its rarity precludes its designation as a new species. Brenner (1963, p. 91, pl. 38, figs. 6–7) referred tricolpate forms with a coarse reticulum to *Retitricolpites*



TEXT-FIG. 6. Diagrammatic representation of *Tricolpites albiensis* sp. nov., $\times 2,000$. a, polar view with exine shown in section on left, nexine black. Surface view of reticulum on right, LO pattern. b, equatorial view, exine in section on left, one colpus shown in centre. Reticulum in surface view on right.

georgensis Brenner, but that species is larger than the English form and has a finer, more closely appressed reticulum. Large reticulate forms from the Patapsco Formation were assigned to *R. geranioides* (Couper) by Brenner (pl. 38, fig. 8; pl. 39, fig. 1), a species originally described from the Miocene of New Zealand. This form, in addition to being much larger than the British species, has a more complex reticulum.

Distribution. From Sample F312 only, Lulworth Cove, Upper Albian.

Tricolpites sp. 2

Plate 81, figs. 23, 24

Description. Grains tricolpate, oval in equatorial view, trilobate and radially symmetrical in polar view. Colpi simple, margins smooth, extremities pointed. Exine baculate, bacula expanded at their extremities and fused to form a microreticulum of mesh diameter $0.5\text{--}1.0\ \mu$. Sexine approximately $0.8\text{--}1.0\ \mu$ thick, i.e. about twice as thick as nexine.

Dimensions. Polar diameter $21\text{--}27\ \mu$, equatorial diameter $18\text{--}24\ \mu$ (5 specimens).

Comparison. The grains described above are fairly close to those designated *Tricolpopollenites virgens* Groot, Penny, and Groot. Brenner (1963, p. 92, pl. 39, figs. 4, 5) reassigned the species to *Retitricolpites* although the specimens described by Brenner possess a finer reticulum than that described by the original authors.

Distribution. On the basis of five specimens distributional records are only provisional. The chief interest of the grain lies in the fact that it appears to be the earliest occurrence of tricolpate grains encountered during this study. It has been recorded only from Leighton Buzzard, in the uppermost sample from the Woburn Sands (Sample F270) and in one sample from the overlying Gault. The first occurrence is thus in the Lower Albian. Associated with the tricolpate grains are well-preserved specimens of *Clavatipollenites rotundus*.

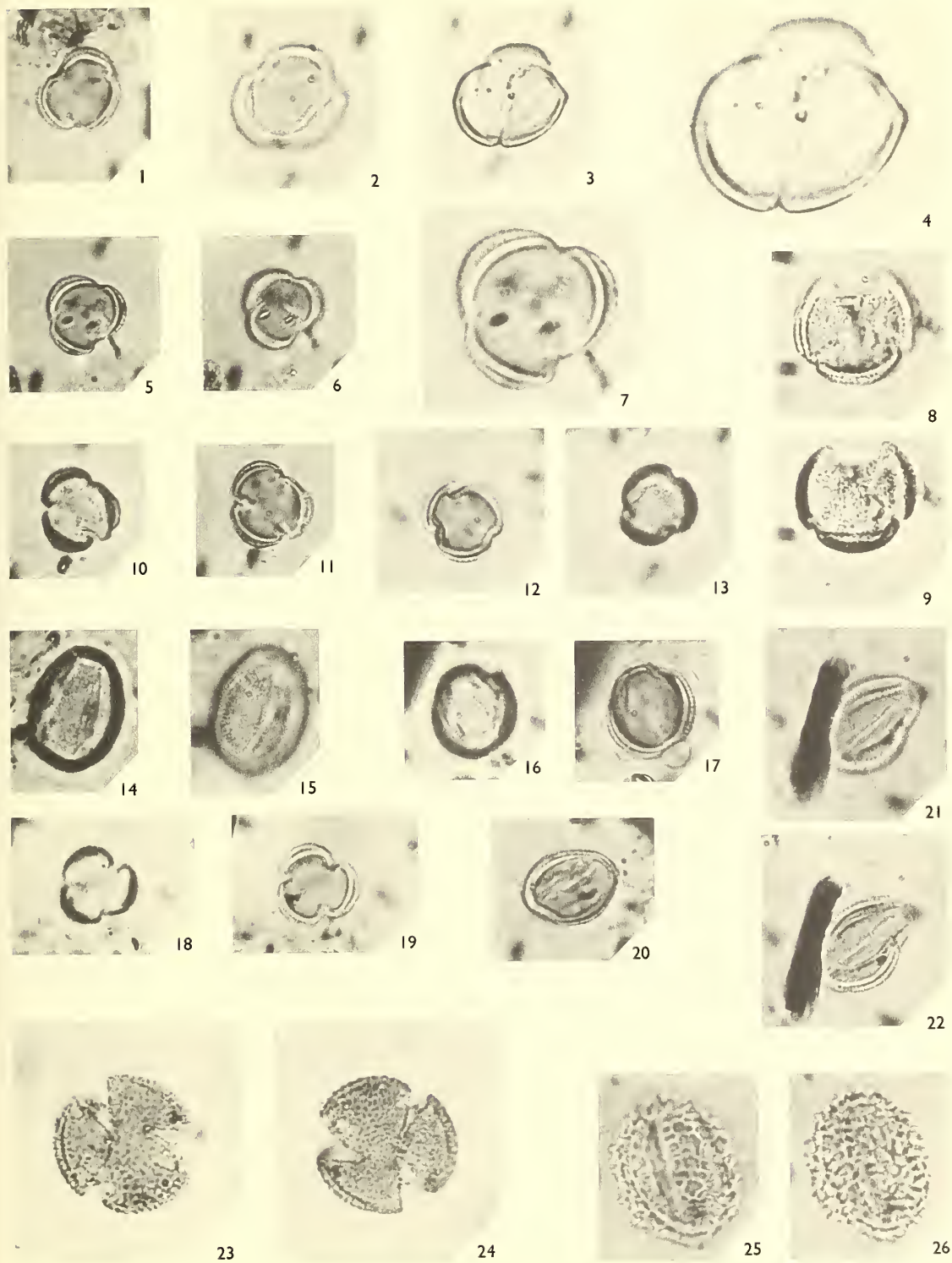
EXPLANATION OF PLATE 81

All figures at magnification $\times 1,000$, unless otherwise stated.

Figs. 1–22. *Tricolpites albiensis* sp. nov. All specimens are from Sample F312, Upper Greensand, Lulworth Cove, Dorset; Upper Albian. 1, F312/4; $49.8, 90.8$; equatorial focus. 2–4, F312/4; $46.8, 90.0$; Holotype, grain slightly oblique. 2, High focus showing microreticulum. 3, Focus on pole showing colpi almost meeting. 4, The same, $\times 2,000$. 5–7, F312/5; $37.0, 99.7$. 5, Equatorial focus. 6, Higher focus approaching pole. 7, Equatorial focus showing bacula, $\times 2,000$. 8, 9, F312/4; $43.6, 96.4$; specimen torn along one colpus. 8, Near equatorial focus. 9, High focus. 10, 11, F312/5; $20.0, 102.0$. 10, High focus close to pole. 11, Equatorial focus. 12, 13, F312/5; $24.9, 95.0$. 12, Equatorial focus. 13, High focus on polar area. 14, 15, F312/5; $33.0, 93.1$; equatorial view. 14, Deep focus on two colpi. 15, High focus on one colpus, microreticulum distinct. 16, 17, F312/5; $29.2, 93.2$; obliquely orientated specimen. 16, High focus showing two colpi. 17, Median focus showing exine stratification. 18, 19, F312/4; $34.9, 89.4$; polar view. 18, High focus. 19, Equatorial focus. 20, F312/5; $33.8, 98.4$; equatorial view, median focus. 21, 22, F312/3; $41.0, 90.4$; equatorial view. 21, High focus on one colpus. 22, Deep focus on two colpi, exine stratification visible.

Figs. 23, 24. *Tricolpites* sp. 2. F270/6; $58.8, 93.8$; Munday's Hill, Leighton Buzzard; Albian. 23, Focus close to equator. 24, Higher focus close to pole.

Figs. 25, 26. *Tricolpites* sp. 1. F312/3; $47.1, 91.5$; Lulworth Cove; Upper Albian. 25, High focus showing one of the colpi and the coarse reticulum. 26, Deep focus on reverse face of grain.



SUMMARY AND CONCLUSIONS

Tricolpate pollen grains of undisputed angiospermous origin first appear in England in sediments of Middle Albian age (apart from one known occurrence in what is probably the Lower Albian). They do not become abundant enough for formal description until the Upper Albian. Their appearance is pre-dated, in the Aptian or slightly earlier, by monosulcate grains referable to the genus *Clavatipollenites*. Grains belonging to this genus possess a tectate exine which suggests that they have an angiospermous affinity, although other features of the grains are more gymnospermous in nature.

Although the Lower Greensand (Aptian and Lower Albian) has been intensively studied palynologically, it has not yielded any recognizable angiosperm pollens. This is of interest since it was allegedly from this formation that Stopes (1912, 1915) described petrefactions of angiosperm woods of an advanced type. These fossils have frequently been cited as indicating a long, pre-Cretaceous history of development for the angiosperms as a whole. The absence of recognizable angiosperm pollen from the formation is difficult to reconcile with the presence of highly evolved woods.

The early angiosperm grains which appear in the overlying formation are of simple form, tricolpate, with a microreticulate sexine. The grains are all notably small, not exceeding $20\ \mu$ in diameter. Their general lack of specialization and small size is shared by late Lower Cretaceous angiosperm grains recorded from other parts of the globe, notably from North America. This apparent lack of specialization in the earliest angiosperm grains does not readily fit in with the idea of a long pre-Cretaceous history for the group. Rather, grain morphology in the observed earliest occurrences of angiosperm grains is more compatible with the view of an early Cretaceous origin (see Hughes 1961).

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E. M. KEMP

West Australian Petroleum Pty. Ltd.
Perth
Western Australia

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SINDULITES, A NEW GENUS OF THE NUMMULITIDAE (FORAMINIFERIDA)

by F. E. EAMES

ABSTRACT. *Operculina sindensis* L. M. Davies 1927 is made the type of a new genus *Sindulites* (Nummulitidae).

THE subgenus *Chordoperculinoides* Arni 1965 of the genus *Nummulites* was proposed to incorporate all real 'nummulites cordelées', and has as its type species *Operculina bermudezi* Palmer, a Caribbean Palaeocene species. However, Arni (1966) in discussing his subgenus gave two plates of illustrations of what he regarded to be '*Chordoperculinoides bermudezi* (Palmer)', but all his illustrated specimens had their origin in the Palaeocene of Libya. On the other hand, the writer's experience of Palaeocene foraminifera from Libya indicates to him that (a) none of the Libyan specimens illustrated by Arni (1966, pl. 1-2) are either conspecific or congeneric with *O. bermudezi*, and (b) the specimens illustrated by Arni (1966, pl. 2, figs. 9-11) are not the megalospheric generation of the microspheric form he illustrates (*ibid.*, figs. 7-8, 13-14), and probably belong to the genus *Operculina*.

DISCUSSION

The species *O. bermudezi* has been well illustrated by Cole (1953, pl. 1, figs. 5-7; pl. 2, fig. 4; pl. 3, figs. 2-12) and by Sachs (1957, pl. 14). The spiral lamina is coarsely perforate throughout, a feature which has led some authors to suggest that it belongs to the genus *Miscellanea*, but the presence of a well-developed perforate marginal cord precludes placing it in the family Miscellaneidae. The subgenus *Chordoperculinoides* as exemplified by its type species *O. bermudezi* is apparently restricted to the Palaeocene of the Caribbean region.

The species to which the Libyan megalospheric forms illustrated by Arni (1966) belong is known to the writer from work he has carried out on material from West Pakistan, India, and Libya; it is the form originally described by L. M. Davies (1927, *cum syn.*) as '*Operculina sindensis*', a species sometimes referred by some subsequent authors to the genus *Ranikothalia* Caudri, 1944. The species *O. sindensis* is here made the type of a new genus.

Family NUMMULITIDAE de Blainville, 1825

Genus SINDULITES gen. nov.

Type species. *Operculina sindensis* L. M. Davies (1927, p. 274, pl. 19, figs. 10-13), Palaeocene.

Diagnosis. Involute, axial section showing very long alar prolongations; wall structure as in *Nummulites* (i.e. not coarsely perforate except at the marginal cord); septal filaments visibly continuous from margin to centre on external surface; marginal cord

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developed into a strongly swollen and coarsely perforate structure; microspheric form little larger than and similar in form to the rather flat megalospheric form.

Remarks. It was Davies (1952) who first suggested that there might be a link between the Palaeocene larger foraminiferal faunas of the East and West Indies when he described *Ranikothalia sahnii* and its megalospheric form *R. savitriae* from West Africa. This species is very closely related to *S. sindensis*, is obviously congeneric with it, and might perhaps by some be considered conspecific with it. *Nummulites nuttalli* Davies 1927 is the type species of *Ranikothalia*, and it differs from the above forms in lacking a strongly swollen marginal cord and in its megalospheric form (*N. thalicus* Davies 1927) being considerably smaller and more inflated than the microspheric form. Prior to 1927, *N. nuttalli* had been referred to *N. planulatus* (Lamarck), 1804, and the writer considers that both *planulatus* and *nuttalli* are just lenticular *Nummulites* with rather numerous septa and high chambers in equatorial section, and that *Ranikothalia* is a synonym of *Nummulites*.

De Cizancourt and Cuvillier (1954) reported *Nummulites (Operculinoides) bermudezi* (Palmer) from the Palaeocene of Senegal. Only one text-figure, a line drawing of an axial section, was given. There is no indication of the coarse perforations in the spiral lamina, so well illustrated by Cole (1953) and Sachs (1957). De Cizancourt and Cuvillier also recorded several other Caribbean species from the Palaeocene in Senegal, but in all cases the illustrations consisted merely of line drawings, and in all cases but one only an axial section was illustrated. The writer would suggest that it is undesirable to identify firmly in Senegal a nummuloid species from the other side of the world on the basis of an axial section only, without any good indication of the wall structure and characters of the equatorial section.

Haynes (1962) recorded and illustrated from the Palaeocene of Libya a form he referred to as '*Operculina canalifera sindensis* (L. M. Davies)'. The quality and clarity of his illustrations are such that one can be quite sure that the wall structure is the same as that of *O. sindensis* (Davies) and that it lacks the coarse perforations in the spiral lamina so characteristic of *O. bermudezi* and excellently illustrated by Cole (1953) and Sachs (1957). However, Davies considered *O. canalifera* and *O. sindensis* to be different species, and Haynes evidently overlooked the fact that *O. canalifera* is completely evolute, whereas *O. sindensis* is completely involute. From what the writer has seen of these two forms in India and West Pakistan, he can confirm Haynes's identification of the taxon '*sindensis*' in Libya.

Castelain (1965) recorded the occurrence of 'probable' *Operculinoides bermudezi* from the Palaeocene of Senegal, and also the occurrence of four discocyclinid forms: *Discocyclina grimsdalei* Vaughan and Cole, *D. harrisoni* Vaughan, *D. barkeri* Vaughan and Cole, and *D. (vel Pseudophragmina (Atheocyclina)) soldadensis* Vaughan and Cole. There were no descriptions or illustrations at all, and the writer feels that it would be inadvisable to accept these identification of species from the other side of the world without further detailed information.

Arni (1966) recorded *Chordoperculinoides bermudezi* from the Palaeocene of Libya. The microspheric forms illustrated by Arni (1966, pl. 1, figs. 1-6; pl. 2, figs. 7-8, 13-14) have all the characters of the genus *Sindulites* and of the taxon referred to as *sindensis* by Haynes (1962). The megalospheric forms illustrated by Arni (1966, pl. 2, figs. 9-11)

seem to be an *Operculina* rather than the A Form of *S. sindensis*. The megalosphere of *S. sindensis* is fairly large, that of a representative specimen from the Palaeocene of Libya being bilocular, the outside dimensions being: protoconch 0.42×0.34 mm., deuteroconch 0.4×0.21 mm. The Palaeocene in Libya is richly fossiliferous, and quite a number of species of *Operculina* are known to occur in association with *S. sindensis*.

In my opinion the above information lends considerable doubt to the occurrence of Caribbean species of shallow water larger foraminifera in West Africa, and, if correct, it would avoid all the difficulty of trying to understand how they could have got from one side of the Atlantic Ocean to the other. All the forms now suggested to belong to the genus *Sindulites* occur in beds of Palaeocene age, the genus being known from West Pakistan, Somalia (unpublished information), Iran (unpublished information), Iraq (unpublished information), Libya, Sicily (unpublished information), and Togoland. It is relatively easy to comprehend how these species of *Sindulites* could have developed as a closely knit group in geographical continuity during Palaeocene times when it is recalled that the Palaeocene sea with its faunas extended from Indonesia through Burma and West Pakistan to the Middle East and East Africa, thereon through Egypt and Libya and the Sahara (Lake Tchad) to West Africa.

The species *sindensis* has at various times been referred to the genera *Operculina*, *Operculinoides*, *Nummulites*, *Ranikothalia*, *Miscellanea*, and the subgenus *Chordoperculinoides*, and now to the new genus *Sindulites*; the reasons why the species *sindensis* should not be referred to any of the first six taxa are:

(a) Except occasionally for the first whorl or two, *Operculina* is completely evolute, whereas *sindensis* is completely involute.

(b) *Operculinoides* and *Operculinuella*, both of which are synonyms of *Palaeonummulites*, are miniature forms, even the microspheric form of which rarely exceeds 5 mm. in diameter, the nucleoconch of the megalospheric form rarely exceeding 0.15 mm.; *sindensis* is quite large, has a double nucleoconch each chamber of which is large, attaining a diameter of 0.4 mm. approximately, and the species possesses a very strongly swollen marginal cord which is not present in *Palaeonummulites*.

(c) *Nummulites* does not have a very strongly swollen marginal cord, and its megalospheric forms are considerably smaller and often much more inflated than the microspheric forms, in contrast to *sindensis*; on these bases *Ranikothalia* would be a synonym of *Nummulites*.

(d) *Miscellanea* lacks the perforate marginal cord of the Nummulitidae, whereas *sindensis* possesses this; moreover, *Miscellanea* has a coarsely perforate spiral lamina, whereas *sindensis* does not.

(e) In *Chordoperculinoides*, as exemplified by its type species, the spiral lamina is coarsely perforate throughout, whereas it is not in *sindensis*.

For these reasons the writer considers that *Sindulites*, as exemplified by its type species *O. sindensis*, is generically distinct from *Operculina*, *Palaeonummulites* (synonyms *Operculinella* and *Operculinoides*), *Chordoperculinoides*, *Miscellanea*, and *Nummulites* (synonym *Ranikothalia*).

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F. E. EAMES
c/o B.P. Research Centre
Exploration and Production Research Division
Chertsey Road
Sunbury-on-Thames
Middlesex

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A REVISION OF THE CARBONIFEROUS LYCOPOD GENUS *ESKDALIA* KIDSTON

by B. A. THOMAS

ABSTRACT. *Eskdalia minuta* Kidston has previously been described as a fern stem, but closer examination of its macroscopic features and a study of its cuticle shows it to be a ligulate lycopod stem. The genus of Russian paper coal cuticles, *Porodendron* Zalesky, is shown to be a synonym of *Eskdalia*.

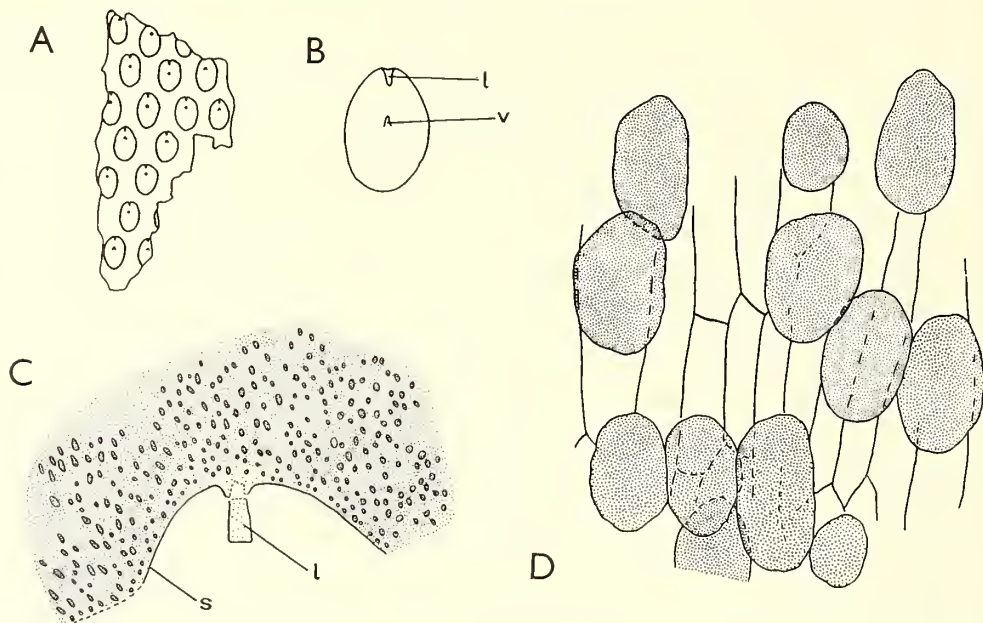
THE type specimen was originally described by Kidston (1883) as *Caulopteris minuta*. This specimen, together with three others, later provided Kidston with the basis for his new genus *Eskdalia* and all four specimens were named *E. minuta*. Kidston still believed them to be probably fern stems, but subsequent examination of the specimens and of their cuticles has shown the species to consist of ligulate lycopod shoots (Chaloner 1967).

Kidston's specimens are the type, No. 5594, Geological Survey, Edinburgh, from Kershope Burn, Liddesdale, Dumfriesshire and Nos. 2739, 2740, and 6731, Kidston collection, Geological Survey and Museum, London, from Clencartholm, Eskdale, Dumfriesshire. The species has also been recorded from the river Coquet, half a mile north-north-east of Holystones, Northumberland (Kidston 1903, p. 820). The known distribution is therefore limited to the Cementstone group of the Lower Carboniferous.

Cuticle was prepared from the type specimen and No. 2740 by macerating portions of coalified compression in concentrated nitric acid and potassium chlorate. Large pieces were obtained from No. 2740 but only small fragments from the type specimen as its carbon split and sometimes completely broke up during maceration. No. 6731 is preserved as an impression so no cuticle could be prepared from it and No. 2739 although a compression gave no cuticle.

Nos. 5594, 2740, and 6731 are large stems but No. 2739 is much narrower than the others and its description is best kept separate. The three large specimens are straight unbranched shoots with oval elongated scars. The stem surface between the scars is flat but ornamented in all three specimens with large numbers of minute lumps, up to 100 μ wide. These lumps are sparsely scattered in No. 5594 but rather more crowded in the other two specimens. No stomatal pits are visible. The leaf scars are in a low-angle spiral of about 10–15° to the horizontal. They are separated from those scars above and below by about a length of a scar and from those on either side by one to two widths of a scar. The scar surface is slightly raised in Nos. 2740 (Pl. 82, figs. 3–5) and 6731 (Pl. 82, fig. 6) but slightly sunken in No. 5594 (Pl. 82, figs. 1, 2). The scars have a sharp margin and the stem cuticle ceases abruptly at this margin, there being none over the surface of the scar; this shows that it is truly a scar. The scar outlines are almost perfectly oval, but may be interrupted at the apex by a slight notch. A minute groove, about 0.4 mm. long and 0.15 mm. wide is sometimes visible running down from the scar apex. These grooves are plainly seen in most of the leaf scars of No. 2740, but not in Nos. 6731 and 5594 where the notch alone is seen in a few scars and there only obscurely. Maceration

of coaly material from the top of the scar proves that a ligule pit is present. It is situated under the groove and is the same shape and size; I imagine that the groove is not an original feature but is caused by a collapse during compression. The cuticle of the ligule pit is attached to the margin of the stem cuticle surrounding the scar (Pl. 82, fig. 7, and text-fig. 1). The vascular prints are shown most clearly in No. 5594 and their structure



TEXT-FIG. 1. *Eskdalia minuta* Kidston. No. 2740, Kidston collection. A, complete specimen showing the arrangement of the leaf scars. $\times 1$. B, single leaf scar showing the position of the underlying ligule pit (l) and the vascular print (v), $\times 4$. C, stem cuticle from the apical region of a leaf scar showing the outline of the leaf scar (s) and the ligule pit cuticle (l). Some, but not all, of the resistant excrescences have been included to give an indication of their size. Slides PF.4417 and PF.4418, $\times 20$. D, stem cuticle showing epidermal cells and overlying resistant excrescences. Slide PF.4417, $\times 300$.

is described and discussed later. In No. 2740 the vascular prints are very faint, being only visible as raised ridges, and in No. 6731 they are indistinguishable.

The fourth stem figured by Kidston (No. 2739) is much narrower than the other specimens, being only 4 mm. broad. The scars are oval and slightly raised but only a few have visible vascular prints and no ligule pits can be seen. The stem surface is smooth possessing no lumps and unfortunately no cuticle could be prepared to show epidermal details. However, the shedding of leaves on such a small shoot is an important feature and can be taken as evidence of its lycopod affinity.

The cuticles of both Nos. 5594 and 2740 are rather thick. The only cells visible are elongated and have straight, rather finely marked outlines; the anticlinal walls only projecting slightly. In part of the cuticle of both specimens there is a border to the cell outline especially at the cell corners, making the cell interior rounded. The cell surfaces are flat but many solid lumps of resistant matter are present on the outer surface of the cuticle. These are most probably the same as the bulges which ornament the stem

surface. These lumps are oval-rounded, usually slightly elongated, and vary in size to about 100 μ . They are irregularly arranged and in many places partly obscure the underlying epidermal cells. The lumps often overlap and where the cuticle is torn many project beyond the broken edge, suggesting that they are somewhat separate excrescences. In No. 6731, where the stem has been lost and the imprint alone remains, many of these lumps are still embedded in the rock.

DISCUSSION

The reason Kidston gave for believing *Eskdalia* to be a *Caulopteris*-like stem was that he thought the vascular prints to be horseshoe shaped. The lower part of the holotype clearly shows oval areas within each leaf scar which are often interrupted at the apex to resemble horseshoes and are evidently the features referred to by Kidston. These 'horseshoes' are raised, but it must be made clear that the lower half of the specimen is really an impression as most of the specimen except a little carbonized material has been lost. Chaloner (1967, p. 525) suggested that they represented matrix infilling of lacunae which more or less surrounded the leaf traces as they passed through the outer cortex. However, the 'horseshoes' and the shallower central areas they surround are entirely carbonaceous. Thus it seems more probable that the 'horseshoes' of Kidston represent the remains of a strong relatively non-compressible tissue. Graham (1935, p. 605, figs. 50, 51) has described such a condition in a lycopod leaf where the xylem and phloem are almost surrounded by an arc of sclerenchyma. This might well have been the condition in *Eskdalia*; Kidston's 'horseshoe' being on this interpretation sclerenchyma and not an arcuate scar as Kidston supposed. The differential compression of the tissues has probably been brought about by the infilling of the stem with mineral matter. In contrast, No. 2740 does not show horseshoe-shaped marks because very little mineral matter ever got inside this specimen and the surfaces came to lie in close proximity like a collapsed tube.

The cuticle of *E. minuta* is very similar to that described from the Russian paper coal of the Lower Carboniferous of the Moscow basin. Both are flat sheets with regularly spaced perforations marking the positions of leaf scars. A small tube of cuticle hangs from the edge of the cuticle at the apex of each perforation. These tubes of cuticle were originally described as rolled up portions of leaf cuticle (e.g. Zeiller 1882, Zalesky 1915) or rolled up cuticle which had formed over the leaf abscission area (Bode 1929). However, Walton (1925) and Wilson (1931) have shown them to be really the internal linings of ligule pits. The Russian cuticles have been given various names. They were originally described as a species of *Lepidodendron* by Eichwald (1860), Auerbach and Trautschold (1860), and Göeppert (1861), then as *Bothrodendron punctatum* by Zeiller (1880, 1882), but Zalesky (1915) instituted a new genus *Porodendron* for them and is followed in his nomenclature by modern Russian workers (e.g. Orlov 1963). Nathorst (1894) had suggested *Porodendron* as a possible alternative name to *Bothrodendron* but did not finally use it, nor did he give it a diagnosis. He should not, therefore, be regarded as its author as quoted by Bode (1929). The species of *Porodendron* have been defined on leaf scar shape which varies from round to oval or heart-shaped and on the structure of the epidermal cells which are normally hexagonal, isodiametric, or slightly elongated. No species has been described with any resistant excrescences on their outer surface.

Distinction between the Russian paper coal cuticles and that from *E. minuta* is therefore limited to leaf scar shape, epidermal cell shape and size and presence or absence of resistant excrescences. Such differences are of value only at the specific and not the generic level and thus *Porodendron* Zalessky is a synonym of *Eskdalia* Kidston.

Nathorst (1914) described a small lycopod cone compression as *Porostrobus zeilleri* believing it to be the fructification of *Porodendron*. Bhardwaj (1958) has subsequently shown the holotype to be heterosporous as might have been expected for a ligulate shoot such as *Porodendron* (= *Eskdalia*). However, as Chaloner (1962, p. 83) has already pointed out, the cone was not found in organic connexion with the stem and mere association is not sufficient evidence for believing them to be parts of the same plant.

SYSTEMATIC DESCRIPTION

Genus *Eskdalia* Kidston

- 1903 *Eskdalia* Kidston, p. 750.
- 1909 *Porodendron* Zalessky, p. 5.
- 1914 *Porodendron* Zalessky; Nathorst, p. 68.
- 1929 *Porodendron* Nathorst (non Zalessky); Bode, p. 134.

Type species. *Caulopteris minuta* Kidston, p. 541, pl. 31, figs. 1, 1a.

Emended diagnosis. Lycopod stem with round-oval or heart-shaped leaf scars in low angle spirals. Leaf scars almost level with stem surface. Ligule pit at apex of leaf scar and projecting beneath it, forming a narrow cutinized tube. One simple vascular print present slightly above middle of leaf scar. No parichnos present.

Eskdalia minuta Kidston

Plate 82, figs. 1-9; text-fig. 1

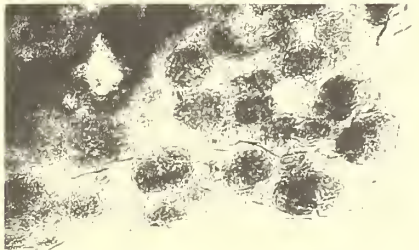
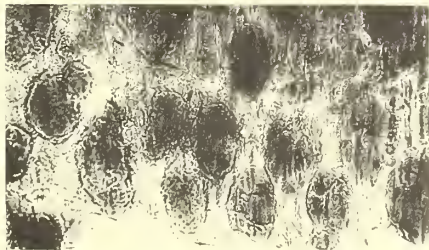
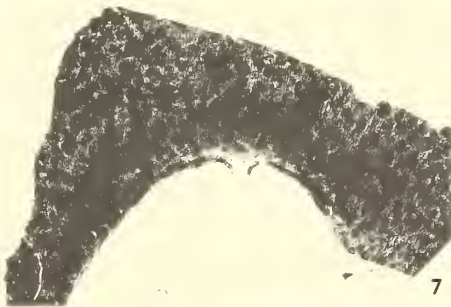
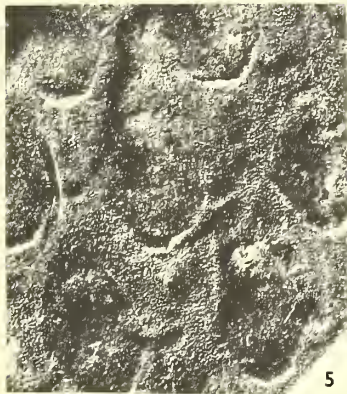
- 1883 *Caulopteris minuta* Kidston, p. 541, pl. 31, figs. 1, 1a.
- 1903 *Eskdalia minuta* Kidston, pp. 750, 820, pl. 1, figs. 4-8.
- 1967 *Eskdalia minuta* Kidston; Chaloner, pp. 525-6, fig. 361.

Holotype. Specimen No. 5594, Geological Survey of Scotland, Edinburgh.

Emended diagnosis. Leaf scars oval, length about one and a half times breadth. Scars separated from those above and below by about a scar length, from those on either side by one to two scar widths. Epidermal cells elongated, about 130 μ long, 25-35 μ broad. Anticlinal walls 1 μ thick, straight, smooth. Periclinal walls flat. Surface bearing

EXPLANATION OF PLATE 82

Figs. 1-9. *Eskdalia minuta* Kidston. 1, 2. Holotype, No. 5594, Geological Survey, Edinburgh. 1, Near side of specimen visible in upper half and the impression of its far side in the lower half, $\times 1$. 2, Portion showing the structure of the leaf scars and vascular prints, $\times 3\frac{1}{2}$. 3-5, No. 2740, Kidston collection. 3, Complete specimen, $\times 1$. 4, 5, Parts of bark surface showing leaf scar and stem details, $\times 4$. 4, Illuminated from above to show leaf scars and vascular prints. 5, Illuminated from below to show ligule pits and surface markings between the leaf scars. 6, No. 6731, Kidston collection, $\times 1$. 7-9, Cuticle from No. 2740. 7, Cuticle from immediately above a leaf scar showing the outline of the scar and point of attachment of a broken ligule pit, $\times 20$. 8, 9, Cuticle showing cellular detail and the resistant excrescences on the outer surface, $\times 100$. Slide PF.4417.



resistant lumps up to about $100 \times 50 \mu$. No stomata. Ligule pit about 400μ long, 150μ broad with rectangular cells $15\text{--}20 \mu$ long, 20μ broad in longitudinal files. Anticlinal walls 1μ thick, straight, smooth. Periclinal walls flat, smooth.

Stratigraphic occurrence. Cementstone Group, Calcareous Sandstone Measures, Lower Carboniferous Limestone Series of Northern England and Southern Scotland.

COMPARISON

There are many other arborescent lycopod genera rather similar to *Eskdalia*. Of these *Cyclostigma* Haughton, *Pinakodendron* Weiss, *Scutellocladus* Lele and Walton, and *Angarodendron* Zalessky are described as eligulate and thus differ in a very important respect. *Bothrodendron* Lindley and Hutton differs in having parichnos prints on the leaf scar. Moreover, most of the species of this genus have the ligule pits situated a little above the leaf scar and separated from it by a narrow band of stem epidermis. The described epidermises of *Bothrodendron* also differ in having many stomata (Thomas 1967).

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B. A. THOMAS
Department of Botany
The University
Newcastle upon Tyne 1

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A SPECIES OF COMPRESSED LYCOPOD SPOROPHYLL FROM THE UPPER COAL MEASURES OF SOMERSET

by M. C. BOULTER

ABSTRACT. Compression fossils of a new species of Lycopod sporophyll, *Lepidostrobophyllum alatum*, are interpreted in terms of their compression history. Three superficially different types of fossil are assigned to the same species as a result of this interpretation. These, it is suggested, are determined by the original orientation of the sporophylls in the sediment prior to compression; either upright, inverted, or lateral. The species has an alated pedicel, and the evolutionary significance of this is discussed.

THE appearance of plant compression fossils, as seen on a broken rock surface, is governed by three factors. First, the orientation of the plant organ in the original sediment; second, the collapse of the fossil resulting from compaction of the matrix; and third, the actual face of the fossil which is revealed by cleavage of the sediment.

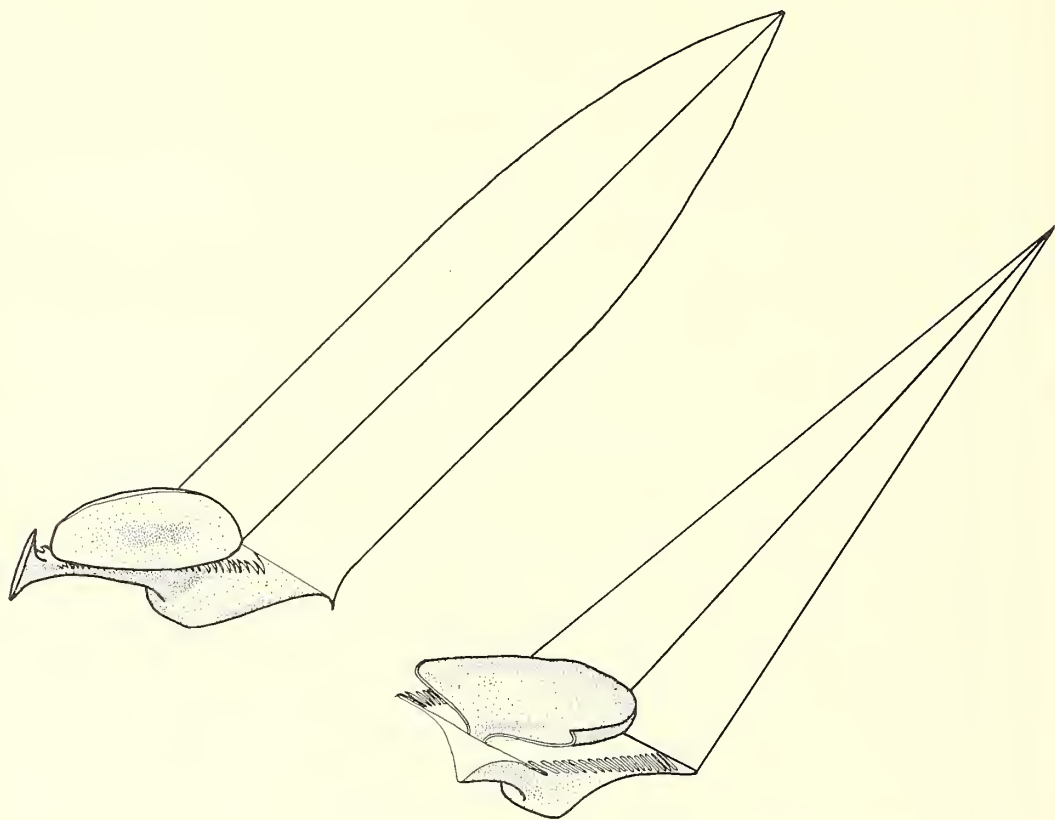
This paper is an account of some Carboniferous lycopod sporophylls, assigned to *Lepidostrobophyllum* Hirmer 1928, the varied appearance of which is interpreted in terms of these three factors.

An interpretation of the original form of the sporophyll described here is shown in text-figs. 1 and 2. Its general character is that frequently demonstrated for petrified *Lepidostrobus* (Balbach 1966, Snigirevskaya 1964, Scott 1920) and for compressed sporophylls (Abbott 1963, Allen 1961) in which a distal leaf-like lamina extends from a shorter proximal region, called the pedicel. The end of this pedicel region was originally attached to the strobilar axis. Such a sporophyll could have fallen into the Carboniferous mud in three different orientations; in the first, the sporophyll remained more or less upright; in the second, it settled in an inverted position (the lower surface uppermost); in the third, it settled on its side so that the lamina of the sporophyll came to lie more or less on edge in the matrix. These three states are here described as upright, inverted, and lateral, respectively (text-fig. 3).

Walton (1936) suggests that the appearance of plant compression fossils is determined primarily by the original shape of the organ's undersurface in the matrix. On this basis, the present sporophylls, together with the matrix of mud, were subjected to vertical compression from the weight of overlying sediment, which compressed the vertical structure but left the horizontal outlines more or less unchanged. Accordingly, it is here suggested that the upright, inverted, and lateral states of orientation in the sediment resulted in the sporophylls being compressed in different ways, depending on the shape of the lower surface in the mud (text-fig. 3).

Splitting of the rock will roughly follow the bedding, and will expose the plant itself by cleaving along the plane of weakness represented by the coaly layer (or layers) of the fossil. The fossil is accordingly represented by an upper counterpart and a lower counter-

part. The three orientation states and these two counterparts mean that a sporophyll may be represented by six different possible states on an exposed rock surface (text-fig. 3). Even more fossil states can exist, due to there being two layers of coal in the collapsed proximal region of the sporophyll, one representing the collapsed pedicel, and the other the collapsed sporangium wall (text-fig. 2). The rock may cleave along either the coaly



TEXT-FIG. 1.

TEXT-FIG. 2.

TEXT-FIG. 1. Reconstruction of *Lepidostrobophyllum alatum*. A large sporophyll which it is suggested would fall in an inverted position in the substratum.

TEXT-FIG. 2. Reconstruction of *Lepidostrobophyllum alatum*. A small sporophyll which would fall in an upright position in the substratum. The dehiscid sporangium is shown in section at the proximal end. This line of section can be compared to Plate 84, fig. 6.

layers of the pedicel (Pl. 84, figs. 1 and 5) or along the coaly layers of the sporangium wall (Pl. 84, fig. 3), giving two quite different fossil forms to the pedicel region. Alternatively, the exposure of the fossil might have started by cleavage along the coaly layer of the pedicel surface, which then jumped across to cleave along the sporangium wall

layer (Pl. 84, fig. 3). On this interpretation it can be seen that a single species of sporophyll can be represented by several fossilization states of rather different appearance.

As might be supposed, the frequency of occurrence of the upright, inverted and lateral states is not random. The frequency of one orientation against another will be governed by the mechanical properties of the sporophyll (centre of gravity, hydrodynamic properties), the physical properties of the Carboniferous sediment (mud, sand, etc.), and by the environment of deposition (speed of deposition, current action). A sporophyll with a small lamina is most likely to fall upright, since the centre of gravity is at the lower part of the pedicel region. A sporophyll with a larger lamina will have its centre of gravity at the upper part of the pedicel region, and so will more readily fall either inverted or laterally. A sporophyll with a tall, narrow sporangium is more likely to fall in a lateral position.

Acknowledgement. I am indebted to Dr. W. G. Chaloner, University College London, for suggesting this topic, and for numerous discussions thereon.

METHODS

Specimens were photographed macroscopically under xylol. An adaptation to Walton's transfer technique (Walton 1923) prepared selected specimens for microscopic examination. A 4 mm. layer of Ceemar embedding resin was poured into a polythene mould. After about one hour, when the surface became tacky, the fossil was placed face downwards on the resin surface. A further 1 mm. layer of resin was immediately poured on to the tacky resin. When the absence of air bubbles was ensured, the block was left overnight to set, and then immersed in hydrofluoric acid in the usual way. This adapted technique yields results as good as Walton's original canada balsam method, and has the advantage that there is no problem of temperature control in the balsam 'cooking' process. A recent detailed description of plastic transfers of fossil plant compressions (Cridland and Williams 1966) is essentially similar to the method used here. In order to investigate parts of the fossils concealed in the matrix (e.g. the heel and sporangium wall), specimens were cut and smoothed in the relevant position at a surface perpendicular to the bedding plane. When viewed under xylol, these sections show considerable detail (Pl. 84, fig. 6). Selling (1944) used a similar procedure to examine Calamitean cone compressions, though he used a microtome to produce thin sections. Block sections such as were used in this investigation require no preliminary softening treatment, and produce results similar to those of Selling. Maceration was attempted, but did not reveal cuticle or spores in any specimen.

THE GENUS *LEPIDOSTROBOPHYLLUM*

Brongniart (1828) instituted the genera *Lepidostrobus* and *Lepidophyllum* to describe respectively the supposed cones and isolated leaves of *Lepidodendron*. Later authors used *Lepidostrobus* and *Lepidophyllum* rather indiscriminately for what were believed to be isolated cone scales (i.e. sporophylls) of *Lepidodendron*. Arber (1922) in a revision of British *Lepidostrobus* compressions referred many of the species based on isolated sporophylls to *Lepidostrobus*, arguing that they are not foliar leaves, as was at one time thought, but the sporophylls of a cone. Hirmer (1928) subsequently set up the genus

Lepidostrobophyllum for those species which were based on isolated sporophylls, using *L. major* as type species. He retained *Lepidophyllum* for what were believed (from lack of a basal sporangium) to be vegetative leaves. Snigirevskaya (1958) has recently pointed out that *Lepidophyllum* was invalid in its application to fossils (having previously been used for a living plant) and substituted the generic name *Lepidophylloides* for vegetative lepidodendroid leaves. Allen (1961) emended *Lepidostrobophyllum* to describe a species of sporophyll containing a number of large megasporos.

Abbott (1963) introduced two new genera to describe unisexual lycopod strobili and their isolated sporophylls, megasporangiate, or microsporangiate. *Lepidostrobopsis* has a horizontally alated pedicel, but otherwise is similar to *Lepidostrobos*. *Lepidocarpopsis* has a horizontal and upturned alation to the pedicel, much wider than the lamina, and bears *Cystosporites* type megasporos or *Lycospora* type microspores. Abbott regards *Lepidocarpopsis* as being 'closer to genus *Lepidocarpon* than *Lepidostrobos*'. A later section in this paper explains why the name *Lepidostrobophyllum* is used for the specimens described here.

SYSTEMATIC DESCRIPTION

Class LYCOPSIDA

Order LEPIDODENDRALES

Genus LEPIDOSTROBOPHYLLUM Hirmer 1928

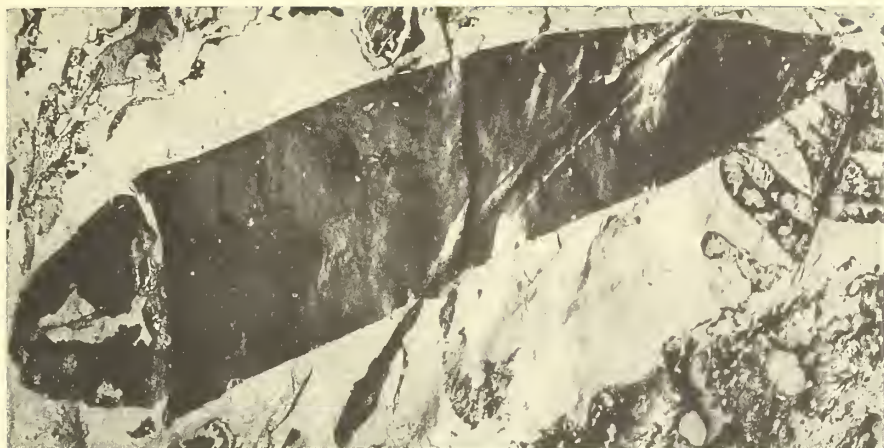
Lepidostrobophyllum alatum sp. nov.

Plate 83, figs. 1-8; Plate 84, figs. 1-10

Diagnosis. Isolated sporophylls consisting of distal lamina and proximal pedicel. Lamina: 1.0-5.0 cm. long; 0.4-1.0 cm. wide at base, directed obliquely towards apex. Central mid-rib extending the whole length of the lamina. Pedicel: 0.4-1.2 cm. long, 0.4-1.0 cm. wide at edge joining lamina. Prominent keel on whole length of lower surface. Heel on lower surface at junction with lamina. Hairy alation at edges, hairs up to

EXPLANATION OF PLATE 83

Figs. 1-8. *Lepidostrobophyllum alatum* sp. nov., specimens compressed in the inverted state. All the specimens figured are in the Geological Survey collection, South Kensington, London. Specimens in figs. 1, 2, 3, 6, 7, and 8 were photographed under xylol, and figs. 4 and 5 in air. 1, Upper counterpart with hastate base to lamina, and prominent sporangium wall at pedicel region; RC 4829, $\times 5$. 2, Syntype; upper counterpart specimen in which the coal layer of the pedicel has broken away, presumably on to the fossil's lower counterpart. The outer part of the sporangium wall remains on this specimen as can be seen at the right hand side of the figure; RC 4830, $\times 5$. 3, Smallest specimen of the inverted type which was collected; lamina mid-rib is seen to protrude down into the shale, and pedicel region is at a lower level than lamina, therefore a specimen from a lower counterpart; RC 4831, $\times 5$. 4, Transfer of pedicel region. The hastate lamina and the mid-rib are seen on the right; the hairy pedicel alation leads to the heel, which protrudes upwards (transfer of upper counterpart); RC 4832, $\times 6$. 5, Margin of lamina, showing teeth pointing towards apex; RC 4832, $\times 100$. 6, longitudinal section of upper counterpart showing step between lamina (on left) and pedicel, and the heel embedded in the matrix; RC 4833, $\times 30$. 7, Transverse section across pedicel region of a lower counterpart, showing one side of the sporangium wall extending just below the surface of the cleavage plane; RC 4834, $\times 12$. 8, Transverse section across pedicel region as in fig. 7; RC 4835, $\times 12$.



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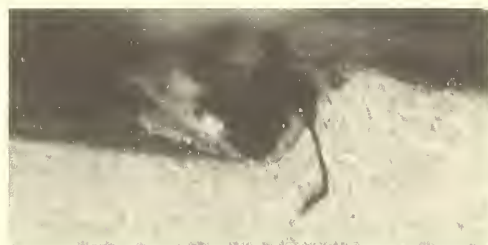
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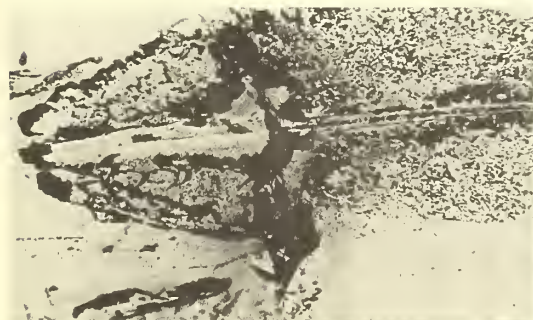
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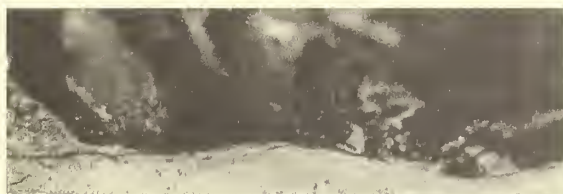
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8

3 mm. long. Sporangium wall extending laterally from pedicel, semi-rhomboidal in transverse section. No spores have been found.

Locality. Tip heap, Kilmersden Colliery, Radstock, Somerset. For the past twelve years, this colliery has been working the no. 10 seam, which occurs in the Farrington Group of the Upper Coal Measures, and represents Plant Zone H of Dix's divisions (Dix 1934). There is no doubt that the sporophylls described in this paper come from within this group.

Syntypes. RC 4830, Pl. 83, fig. 2; RC 4837, Pl. 84, fig. 2; Geological Survey, London.

Description of sporophylls oriented in the upright state. Detached sporophylls which are seen in this state consist of two parts, the distal part or lamina, and the proximal part which was originally attached to the strobilar axis, called the pedicel. The lamina is of variable size, 1.0–4.2 cm. long and 0.4–0.7 cm. wide at the base. The lateral margins are more or less straight, and have teeth about 0.2 mm. long, pointing towards the apex (Pl. 83, fig. 5). The mid-rib, which is about 0.7 mm. wide, passes from the base to the apex, and is made up of two parallel ridges (Pl. 84, figs. 1, 2).

The pedicel is of variable size, 0.4–1.0 cm. long, and 0.4–0.7 cm. wide at the edge joining the lamina, tapering down in nearly all specimens to 0.2 cm. wide at the proximal end. A hairy alation extends from each of the lateral margins, the hairs being up to 3 mm. long at the distal end (Pl. 84, fig. 4). These hairs are best seen in transfers, but in many of the specimens which were studied during this investigation they were not preserved. The keel extends for the whole length of the pedicel, and protrudes either upwards or downwards in upper or lower counterparts respectively. It develops into a heel at the juncture with the lamina, as can be seen in section (Pl. 84, fig. 7). The sporangium wall is preserved as two lobes, one on either side of the pedicel, and extending further than the pedicel alation (Pl. 84, fig. 4). Transverse sections across the pedicel reveal the sporangium wall embedded in the matrix (Pl. 84, fig. 6), though, as would be expected, this is only seen on the upper counterpart specimens.

Description of sporophylls oriented in the inverted state. The lamina is of variable size, 2.0–4.8 cm. long, 0.6–1.0 cm. wide at the base. The lateral margins are parallel for about the first two thirds of the length; then they curve to form an acuminate apex. Just as in the upright state specimens, these have a serrate edge and a mid-rib, though in the inverted state the lamina is hastate at the base (Pl. 83, figs. 1 and 4). The pedicel is of variable size, 0.7–1.2 cm. at the distal end. As in the upright state specimens, the pedicel has a hairy alation, though here the hairs are slightly thicker and less regular (Pl. 83, fig. 4). Collapse, during compression, has taken place into the (open) sporangium, and so the sporangium wall is more prominent in this type of preservation than in the upright orientation state. Transverse sections of some lower counterpart specimens show the embedded sporangium wall (Pl. 83, figs. 7, 8), though this is often absent when cleavage has occurred along the plane of the wall. There is a difference in level between the lamina and pedicel of up to 2 mm. On the lower counterpart the lamina is on a higher level than the pedicel, whilst on the upper counterpart the lamina is lower than the pedicel.

Description of sporophylls oriented in the lateral state. The lamina is from 1.0 to 3.0 cm. long. The distal end is often broken by cleavage or concealed in the rock. It is preserved

so as to lie more or less perpendicular to the bedding plane, and so is preserved on the cleaved rock face only as a narrow line, or steeply dipping surface of about 3 mm. width. Such characters as the original width, the serrate margin, and the mid-rib cannot be seen. The pedicel proper is from 2 to 4 mm. high throughout its whole length (Pl. 84, fig. 8). On the lower edge the keel is about 3 mm. deep in the centre, becoming deeper at the proximal end for attachment to the strobilar axis. It is also deeper at the distal end where it forms the heel (Pl. 84, fig. 9). The sporangium wall extends from 0.5 to 1.0 cm. above the whole length of the upper surface of the pedicel (Pl. 84, figs. 8–10).

INTERPRETATION OF THE FOSSIL STRUCTURES

It was explained at the beginning of this paper that the appearance of the sporophyll fossils has been determined by the original shape of the undersurface in the mud. The sporophyll could have fallen in the mud in three principal orientations, each with a different undersurface, and these are correlated with the three different fossil states of the original structure which are found to occur.

Sporophylls falling into the mud in an upright position have the keel, heel, lower pedicel surface, pedicel alation, the outer extremity of the dehiscent sporangium wall, and the entire lamina, making up the lower surface in the matrix. These structures have been preserved without distortion in the horizontal plane. The original upper surface of the pedicel and the inner parts of the sporangium wall will collapse to the level of the lower surface. But since the sporangium was semi-rhomboidal in transverse section, it became filled by, and separately enclosed in mud, and so is preserved as a separate extension from the upper surface of the pedicel (text-fig. 3). Thus, we would expect to see the sporangium buried in the matrix of the upper counterpart specimens (Pl. 84, fig. 6). The original adaxial lamina mid-rib is compressed to form a ridge protruding upwards in the matrix.

EXPLANATION OF PLATE 84

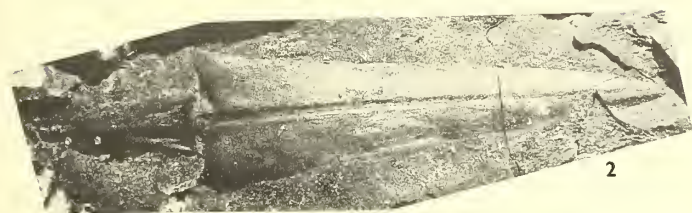
Figs. 1–10. *Lepidostrobophyllum alatum* sp. nov. All specimens figured are in the Geological Survey, London. All but figs. 2 and 4 were photographed under xylol. 1–7, Specimens fossilized in the upright state. 1, Upper counterpart in which the sporangium wall is not visible at the surface; it is suggested in this article that the sporangium wall is embedded in the shale; RC 4836, $\times 4$. 2, Syntype. The lamina mid-rib protrudes into the matrix whilst the pedicel protrudes outwards, suggesting the specimens to be from the upper counterpart; the outer parts of the sporangium wall can be seen passing into the shale; RC 4837, $\times 4$. 3, Upper counterpart. At top left of figure, the sporangium wall extends beyond the pedicel alation; the opposite part of the sporangium wall has not followed the cleavage plane and is embedded in the matrix of the counterpart; RC 4838, $\times 4$. 4, Transfer showing hairy alation to pedicel and sporangium wall extending beyond this alation; RC 4839, $\times 4$. 5, Small specimen from lower counterpart with no sporangium wall; RC 4840, $\times 4$. 6, Transverse section of upper counterpart across pedicel region, showing the two lobes of the sporangium wall embedded in the matrix; RC 4841, $\times 20$. 7, Longitudinal section of lower counterpart; heel prominent, and no step between lamina and pedicel; RC 4842, $\times 20$. 8–10, Specimens fossilized in the lateral state. The lamina is broken off in three specimens (top left in 8 and 10, top right in 9). 8, Pedicel alation extends to half way up the sporangium wall; RC 4843, $\times 4$. 9, Sporangium wall almost three times higher than the pedicel alation; heel (bottom right) and keel are prominent below the pedicel; RC 4844, $\times 4$. 10, Specimen showing further variation in the size of the sporangium wall; RC 4845, $\times 4$.



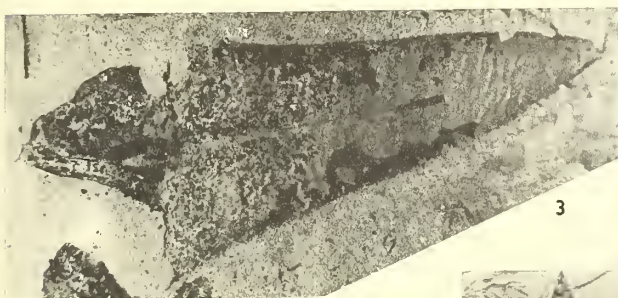
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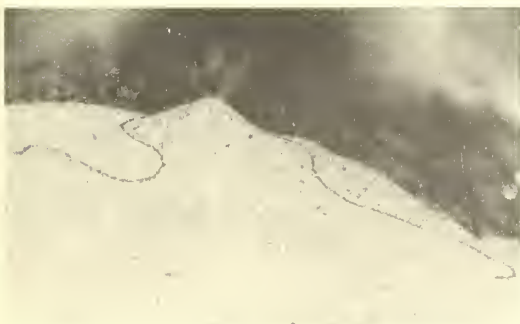
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6



10

	transverse sections of pedicel region			transverse sections of lamina			of sporophyll	
	upright	inverted	lateral	upright	inverted	lateral	upright	inverted
original structure								
structure compressed in sediment								
upper counterpart after cleavage								
lower counterpart after cleavage								

TEXT-FIG. 3. Diagrammatic sections of *Lepidostrobyllum alatum* describing the consequences of the compression process. Sections across the matrix shown by stippling. Compression of the original sporophyll produces structures shown in the second horizontal row of drawings; for instance, the upper counterpart of upright state sporophylls have a protruding pedicel, a depressed (never protruding) lamina mid-rib, and no step between lamina and pedicel (see drawing of L.S. sporophyll). Again, the upper counterpart of inverted state sporophylls always have a flat pedicel region, a protruding lamina mid-rib, and a step down from the pedicel to the lamina. A specimen with a protruding pedicel (i.e. upright state, upper counterpart) never has a protruding lamina mid-rib, or a step between lamina and pedicel.

For sporophylls which fell in an inverted position, the dehiscent sporangium wall and upper pedicel surface will form the lower compression surface. The pedicel and its hairy alation, together with the sporangium wall, will be preserved. But the position of the sporangium wall in the matrix will be influenced by the pedicel collapsing on top of it. The wall will thus be compressed close to the pedicel surface (Pl. 83, figs. 7, 8). The original lower surface of the pedicel and the keel will collapse on to the underlying pedicel surface and will not be preserved. The heel collapses to a more or less vertical position, but remains separated from the pedicel surface (Pl. 83, fig. 6). The originally adaxial lamina mid-rib collapses into its morphologically upper surface; that is, downwards in the matrix. It is suggested that the step between the lamina and pedicel in these inverted specimens is due to the original morphology at the juncture of lamina and pedicel. Petrified specimens (Arber 1914, pl. 22, fig. 9; pl. 24, fig. 20; pl. 26, fig. 43) show that the distal face of the heel is a straight continuation of the lower surface of the lamina, and that there is a slight depression on the upper surface at the distal end of the lamina, directly above the heel. This is likely to be preserved after compression, as a difference in level between lamina and pedicel (text-fig. 3).

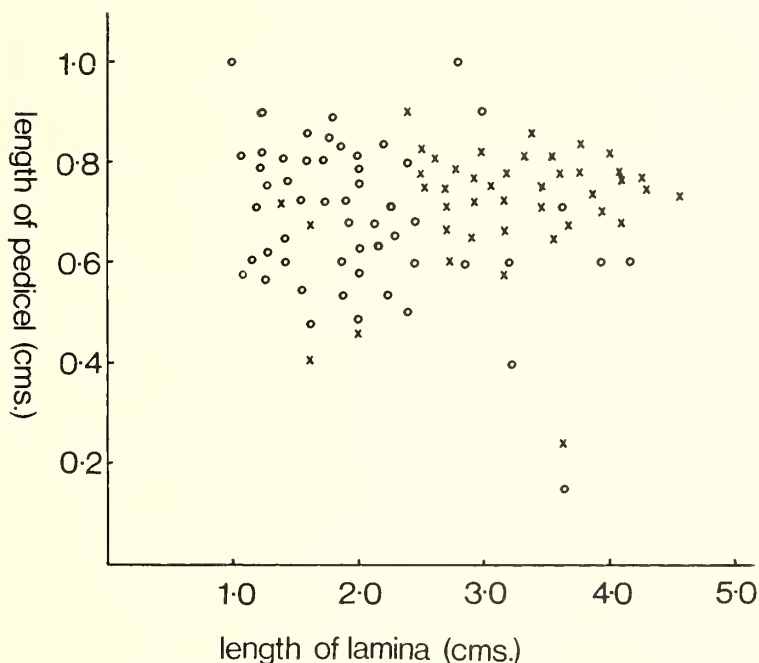
This interpretation is again consistent with the specimens studied. Specimens in which the lamina mid-rib is seen as a groove depressed into the matrix (i.e. in the lower counterpart) have no heel in section, though the sporangium wall can be seen in transverse section (Pl. 83, figs. 7, 8). This is never as well defined as in the upright specimens because, as is suggested above, the pedicel collapses on top of the sporangium wall during the process of compression. And when the mid-rib appears as a ridge projecting upwards from the cleaved fossil surface (i.e. in the upper counterpart) the heel is present in the matrix, as seen in section, and the sporangium wall is absent. The keel is never seen in either upper or lower counterpart fossils and the pedicel surface is always more or less flat.

Sporophylls which fell in the sediment in an upright position tend to have a smaller lamina length pedicel length ratio than those that fell inverted (text-fig. 4). This is presumably because the relatively greater lamina length favoured settling in the inverted position. The size of the sporophyll would probably be a function of its position on the strobilus; the larger sporophylls towards the base, the smaller ones towards the apex. This conclusion is evident from studies on petrified material (Arber 1914, pl. 23, fig. 13).

Specimens of sporophylls which have been compressed laterally show the original vertical aspect of the keel, heel, pedicel, sporangium wall, and lamina. The pedicel alation is preserved in most specimens (Pl. 84, figs. 8, 10) as a rugose margin above the pedicel, a very doubtful consequence of compression of the hairs which are seen in the upright and inverted states. From the evidence available in these compression fossils, it is not possible to ascertain the original morphology of the pedicel alation; whether it was horizontal, or upturned at the edges to protect (even partially) the sporangium. Indeed it must be accepted that the attribution of the laterally compressed specimens to this species (which is based primarily on upright and inverted specimens) is somewhat arbitrary. But at least all three states can be reconciled with a single reconstruction such as that offered in text-fig. 1. Until spores are found enclosed on the sporangium, or other indirect evidence is obtained, the correlation of the sideways compressed fossils with the other two states remains hypothetical.

COMPARISON WITH PREVIOUSLY DESCRIBED SPOROPHYLLS

The majority of specific, and indeed generic, diagnoses of detached lycopod sporophylls are concerned principally with the size and shape of the lamina and pedicel, and in some cases with the type of spore extracted. No spores have been found in the present study, and so the only comparable characters are size and shape. Both these have proved to be



TEXT-FIG. 4. Length of sporophyll lamina plotted against length of pedicel, for specimens of *Lepidostrobohyllum alatum* sp. nov. compressed in upright (o) and inverted (x) states. The distribution shows that the longer lamina give a preferred orientation towards the inverted state (clustering of symbol x at right of diagram).

extremely variable in *Lepidostrobohyllum alatum* and so the comparison with other sporophylls is limited by our ignorance of the details of sporangium and pedicel for most of the earlier described species.

Lepidostrobos triangularis Zeiller. The original description by Zeiller (1886) and subsequent descriptions (Arber 1922, Crookall 1966) show that this species is very similar in shape and size to the smaller specimens described in this paper as having been fossilized in the upright state. The pedicel resembles that in specimens of *L. alatum* which have cleaved across the layer of the pedicel and not along the sporangium wall (Pl. 84, fig. 5). But specimens labelled as *L. triangularis* in the Kidston Collection, Geological Survey, London (nos. 819a, 6249, 8196) show a clearly defined edge to the pedicel, which is too narrow to have alation. Also these specimens have a completely flat contour, and so their compression history cannot be compared to that of *L. alatum*.

Lepidostrobos goodei Jongmans (Jongmans 1931). In his recent review Crookall (1966) describes this species as having a wedge-shaped pedicel 5–7 mm. long and 2–3 mm. wide. This again could represent upright specimens of *L. alatum* in which the pedicel alation and sporangium wall are compressed in the matrix, if they are present at all; sporophylls at the extreme tip of the strobilus may not have had a well-developed alation or sporangium. The lamina of *L. goodei* is of a comparable size to upright specimens of *L. alatum*.

Lepidophyllum gracile Lesquereux. Lesquereux's type figure (Lesquereux 1884) has similar shape and size to upright specimens of *L. alatum* which have cleaved along the sporangium wall. The species has not been described from Britain.

Lepidostrobos brevifolius Lesquereux (Lesquereux 1857). This has a wedge-shaped, keeled pedicel, 0.8–1.0 cm. long, and a triangular lamina, 6–8 mm. long (Crookall 1966). This species can again be compared to small specimens of *L. alatum*.

Lepidostrobos lancifolius Lesquereux. The type figure of this species (Lesquereux 1870) shows identical features to the inverted state of *L. alatum*: acuminate apex to lamina, hastate base to lamina, prominent sporangium wall to pedicel, and similar dimensions. No details are available in the literature of the step between lamina and pedicel or whether the mid-rib formed a ridge or a groove.

Lepidophylloides acuminatus (Lesquereux) Crookall (Crookall, 1966). Although no specimens of *L. alatum* as large as those described for this species have been collected, the shape and proportions of the two species are identical.

Lepidocarpon mazonensis Schopf. Schopf (1938) described a side-compressed sporophyll containing a seed megaspore which has a rugose texture on the margin of the integuments. The comparable structure in laterally compressed specimens of *L. alatum* is what is here regarded as the pedicel alation. Except for the megaspore in Schopf's specimens, the two types seem identical.

If the lateral states of *L. alatum* had a single functional seed megaspore and an integument, rather than the alated pedicel which is suggested in this paper, then they should be reassigned to *Lepidocarpon* sp.

Alternatively the interpretation of the lateral state of *L. alatum* given above could be correct. And if the specimens described by Schopf are equivalent (i.e. they have an alated pedicel rather than an integument), both Schopf's *Lepidocarpon mazonensis* and the specimens described here as *Lepidostrobophyllum alatum* must be reassigned to a different genus, describing sporophylls with a single functional megaspore and no integument, namely *Achlamydocarpon* Schumacker-Lambry (see below).

Thirdly, *L. alatum* may not have contained a single functional megaspore, in which case the present separation of *Lepidostrobophyllum alatum* from *Lepidocarpon* sp. holds good.

Cantheliophorus spp. Bassler. This genus (Bassler 1919), described as a 'sporangiphoric lepidophyte', has a similar appearance to the lateral states of *L. alatum*. Schopf (in Janssen 1940) refers Bassler's genus to *Lepidocarpon* by reinterpreting the structure. This was supported later (Schopf 1941, p. 559) by the identification of single megaspores

from the illustrations in Bassler's paper. Photographs of *Lepidophyllum waldenburgensis* in Nathorst (1914), refigured by Bassler (1919), have a similar character to the specimens of *L. alatum* which were laterally compressed.

All the above-mentioned species are defined principally in terms of size and shape, factors which are variable in *L. alatum*. It is therefore suggested that the specimens described in this paper should not be assigned to any previously described species, unless characters of the pedicel structure and the compression process are investigated for these established species. Unfortunately, it is not possible to transfer or develop type specimens to obtain this information, and so full descriptions of species described over forty years ago are unlikely ever to be obtained. Inevitably, new species must be made which may overlap the ill-defined limits of other species.

GENERIC ATTRIBUTION OF *L. ALATUM*

The assignation of the species here described to *Lepidostrobohyllum* is uncertain, due to the absence of spores in all specimens. If the sporangium is ever found to have contained one or several tetrads of functional megaspores, or numerous microspores, then the assignation is correct. But if the sporangium contained only one functional megaspore, with three aborted spores (i.e. a *Cystosporites* type megaspore), then the sporophylls belong to a genus in the Lepidocarpaceae (Schopf 1941).

In all specimens of *L. alatum* the sporangium wall extends beyond the pedicel alation (Pl. 83, fig. 4; Pl. 84, fig. 4); the alation could never have completely enclosed the sporangium. Therefore the genus *Lepidocarpon* is not applicable to any of the specimens dealt with here.

Schumacker-Lambry (1966) describes a new genus of petrified lepidocarps as *Achlamydocarpon*. The pedicel alation is not developed into an integument, rather, it is as in the species described here, or absent. The single functional megaspore is completely protected by a sporangium wall four layers thick. If a single functional megaspore is ever found in any *L. alatum* specimens, the generic assignation might be changed to *Achlamydocarpon*, though the identification of a thick sporangium wall in compression fossils presents a severe difficulty. It is evidence that Schumacker-Lambry's genus *Achlamydocarpon* may be partially synonymous with Abbott's genus *Lepidocarpopsis*; they both represent 'unintegumented lepidocarps', although the evidence for lack of integument is clearer in Schumacker-Lambry's petrified material than in Abbott's compressions.

In his reinterpretation of Bassler's *Cantheliophorus*, Schopf refers it to the genus *Lepidocarpon*. He did not differentiate between the structures of an alated pedicel and a thick sporangium wall, so it is possible that some, if not all of the specimens described by Bassler are members of *Achlamydocarpon*. In this case, 'the surface rugosity of the sclerotic cells on the integument surface' (Schopf 1941, p. 560) would be cells of the thick sporangium wall, or of the pedicel alation.

EVOLUTIONARY SIGNIFICANCE

The structure of the pedicel in *L. alatum* represents an intermediate stage in the evolutionary change from the unprotected sporangium of many species of *Lepidostrobus*

sporophylls to the integumented *Lepidocarpon*. Abbott (1963) has instituted a new genus for such an intermediate, *Lepidocarpopsis*, whilst Balbach (1966) suggests that the morphological changes involved are only of specific importance.

The evolutionary tendencies towards specialization of the pedicel and sporangium structure in arborescent lycopod sporophylls seems to be more diverse than was previously thought. The simplest Carboniferous *Lepidostrobus* had completely unprotected sporangia containing microspores and megaspores. *Lepidostrobus takhtajanii*, *L. masleni*, and *Achlamydocarpon belgicum* seem to represent one extreme in the evolutionary development with a single fertile megaspore protected by a thick sporangium wall and no integument, whilst *Lepidocarpon*, with a single fertile megaspore protected by an integument around the sporangium, represents another.

The broad extent of the hairy alation in *Lepidostrobohyllum alatum* is in some degree morphologically intermediate between *Lepidostrobus* and *Lepidocarpon*. The lack of information concerning the thickness of the sporangium wall and the type of spores in these specimens make it impossible for us to appreciate the significance of the species, at the present.

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M. C. BOULTER
 Department of Biology
 West Ham College of Technology
 Romford Road, London E. 15

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FUNCTIONAL STUDIES ON THE CRETACEOUS OYSTER *ARCTOSTREA*

by R. M. CARTER

ABSTRACT. The three Cretaceous species-groups *Arctostrea colubrina* (Lamarck), *A. unguolata* (Schlotheim), and *A. diluviana* (Linnaeus) are described. Particular attention is paid to the detailed morphology of *A. colubrina*, from which its life history is reconstructed. It is inferred that the unusual characters of the genus (especially the arcuate shape, the zigzag commissure and the funnel spines) relate to the size and importance of the gills as primary food-collecting organs. The subspecies *A. colubrina ricordeana* (d'Orbigny) possesses, in addition to these special adaptations, a set of long spines secreted sub-parallel to the plane of the commissure on the lower valve; these are interpreted as a specific response to the hazards of inhabiting a substrate of soft ooze. Behavioural and structural adaptations used by Recent oysters for combating conditions of high turbidity are discussed, and it is suggested that similar methods were utilized by many extinct species. Funnel spines occur in other bivalves, including *Pinna* and *Etheria*; it is likely that they also are connected with inhalent current streams. Some taxonomic implications of the functional interpretation of *Arctostrea* are presented in an appendix.

MANY malacologists consider Recent *Ostrea* to represent the peak of bivalvian evolution (e.g. Atkins 1938), and few would dispute that its integrated gill/palp complex represents a feeding organ of outstanding power and efficiency. It is one of the very few Recent bivalve genera for which a large amount of published material is available, owing this distinction mainly to its economic importance. It appears that such spectacular success as oysters have achieved has at least partly been made possible by their adoption of a mode of life involving cementation to a hard substrate. Yet because of their irregular shell form consequent upon such cementation, oysters have understandably always been the *bête noire* of most systematists, palaeontologists included. It is the purpose of this paper to apply some of the available information on Recent *Ostrea* to a study of a distinctive group of extinct oysters in an attempt to better understand their morphology, and hence to clarify their taxonomy. It has become apparent to me during this study that however well known the biology of common European and American oysters may be, there is still a large amount of primary research needed on most of the more exotic tropical oysters before our knowledge of the family can be claimed to be reasonably complete.

The genus to be studied, *Arctostrea*, has its morphology exemplified by the species *A. colubrina* Lamarck, a common oyster in the Cenomanian rocks of Western Europe (Pl. 85, fig. 5). Particularly noteworthy are the superbly developed zigzag commissure (Pl. 86, fig. 1), and the highly characteristic arcuate shape in plan view (Pl. 85, fig. 5). Other groups of oysters have zigzag commissures, and virtually all lineages of oysters from the Jurassic onwards have at some time exhibited a tendency to arcuate shape, but only a relatively small group of species ranging through the Jurassic and Cretaceous was able to combine these two trends into a successfully adapted working complex.

To detail the biological and stratigraphical details of presently known populations of *Arctostrea* is far outside the scope of this paper. For the purposes of morphological description it will suffice to recognize three major infrageneric categories, conveniently termed species groups. They are the *Arctostrea colubrina* group (Pl. 85, fig. 5), the

A. unguata group (Pl. 87, fig. 8), and the *A. diluviana* group (Pl. 85, fig. 1), and will be discussed in turn.

Terminology. In order to facilitate unambiguous discussion of detailed ontogenetic changes, the terms *proximal* and *distal* are preferred to the more normal dorsal and ventral (text-fig. 4); the shell margins are termed the *anterior* and *posterior arcs*. The term 'vertical zone' is useful in description of shells with steep (though not necessarily rigorously vertical) slopes around the valve edge. A vertical zone may occur virtually all round the commissure (as in *Arctostrea colubrina*), or may be limited to specific areas on the commissure (as in *Arctostrea diluviana*). It is the inevitable result of shell secretion along sectors of mantle edge where no mantle cell generation is taking place (see Carter 1967).

Note on captions and material studied. The following abbreviations are used consistently in all plate and text figure captions: UMZC, University Museum of Zoology, Cambridge University; SM, Sedgwick Museum, Cambridge University; BM, British Museum (Natural History), London. It should be emphasized that this study is based upon the examination of specimens in these museum collections; statements as to the type of substrate inhabited by different populations of *Arctostrea* are, in the main, inferences made from the matrix that still adheres to many specimens.

THE *ARCTOSTREA COLUBRINA* GROUP

This species group may be recognized by its regularly arcuate shape (Pl. 85, fig. 5), well-developed vertical zone, the numerous sharp zigzags around the commissure (Pl. 88, fig. 5), and the presence of small tubular spines situated at the crest of each commissural zigzag (Pl. 86, fig. 2); the growth track of these spines results in a characteristic divaricating ornament pattern on the flat shell top. The group was widely distributed, and common, in Lower Cretaceous times, and is known from the Middle East, North Africa, Austria, Germany, France, Portugal, and England.

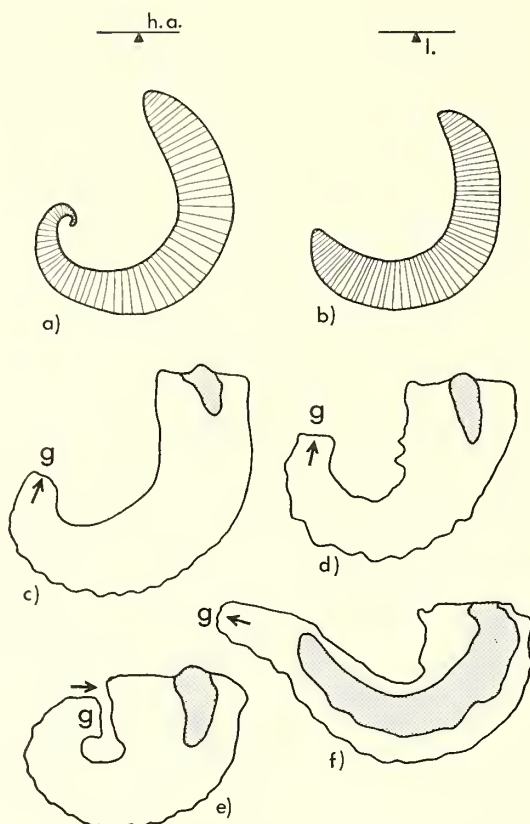
A. colubrina ricordeana (d'Orbigny)

The availability of specimens of *ricordeana* preserving every detail of their life history in the form of well defined growth-lines enables an accurate ontogeny to be reconstructed. Though this reconstruction is based on populations of *colubrina ricordeana* inhabiting the Lower Chalk Sea of England, the greater part of it applies with only minor modifications to other populations of *colubrina* s.s., and also with slightly greater modifications to members of the *ungulata* and *diluviana* species groups.

The Chalk specimens of *ricordeana* are large, often very inflated, oysters with strong zigzag valve edges (Pl. 86, fig. 1). Adult specimens may possess a dimension greater than 110 mm. in the plane of the commissure, and have a maximum transverse dimension ('inflation') of up to 70 mm. During growth, mantle expansion is at a maximum distally on the commissure, in a narrow arc here named the *generative arc* of the mantle edge (text-fig. 1); elsewhere on the commissure, outside of the generative arc, the introduction of new mantle cells is minimal, though not altogether absent. Thus shell secretion during the life of the animal results in the building of a vertical zone around the greater part of the commissure; this vertical zone is crossed by steep plicae that represent the tracks of earlier growth stages of the zigzag commissure (Pl. 86, fig. 2).

The generative arc is not only the site of localized generation of new epithelial cells, it is also the site of introduction of *all* new plicae (Pl. 85, fig. 5). Any zigzag on the current

commissure can always be traced back up its own plica to the point of its inception as a gentle undulation in the generative arc of an earlier commissure (e.g. plica *a*, Pl. 86, fig. 1).



TEXT-FIG. 1. Comparison of the shape of the gill of (a) *Pecten* and (b) *Ostrea* with the adult shell outline of four specimens (c-f inclusive) of *Arctostrea colubrina* (Lamarck). All $\times \frac{1}{2}$.

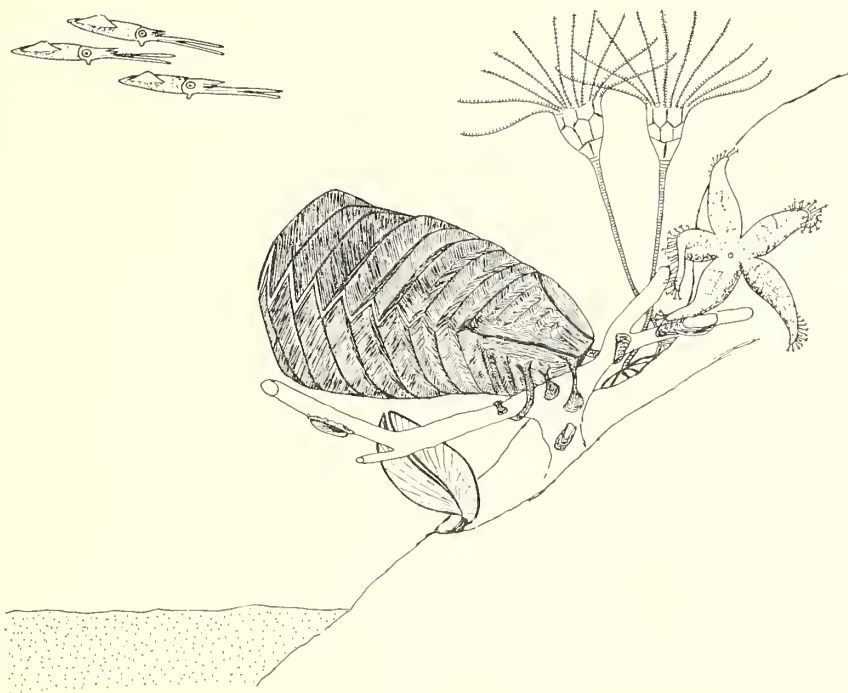
All upper (right) valves viewed from above; stippled area represents the unornamented, pre-zigzag dissoconch, corresponding to the area of attachment on the left valve. *h.a.*, hinge axis; *l.*, ligament pit; *g*, generative arc of the mantle edge, arrow indicating direction of mantle expansion.

Ontogeny. The significant stages in the life history of *ricordeana* are conveniently summarized in discrete steps:

1. Spatfall on to available hard attachment sites; commonly pieces of shell and echinoderm test. This was accompanied by immediate cementation by the surface of the left valve; by analogy with Recent oysters, it was followed in the next few days by metal morphosis from the veliger type organization to the adult anatomical form.

2. Continuing shell secretion eventually resulted in the size of the animal exceeding the size of the attachment object. At some stage after this the mantle edges changed

from being roughly planar to being sharply zigzag, passing through stages from gently flexed to more sharply folded (Pl. 86, fig. 4). This change in the morphology of the mantle edge may have been partly under muscular control, but it was probably also connected with localized epithelial generation. As shell secretion continued unabated, a clear record of these changes is shown by the successive growth-lines on the valve surface. In particular, there is always preserved an unornamented pre-zigzag dissoconch that is



TEXT-FIG. 2. Reconstruction of life position of an early adult *Arctostrea* attached proximally by cementation and root spines.

sharply demarcated from the following growth stages and gives a clear indication of the size and shape of the attachment object (Pl. 88, fig. 3).

3. When the shell outgrew the area of cementation laterally, the mantle edges of the left (lower) valve on either side of the mantle isthmus secreted tubular spines which were attached in a root-like bundle either to the initial attachment object, or to closely adjacent objects (text-fig. 2). These root-spines were first secreted about the time of the inception of the zigzag commissure, and obviously served to attach the animal tightly to the substrate. They continued to be secreted so long as the animal was still attached to the substrate proximally. Some specimens do not progress beyond this ontogenetic stage.

4. At this stage in ontogeny, which occurred at very different shell sizes in different individuals, the shell either broke free from its proximal attachment or, if it was attached to a relatively small object, overbalanced, and hence came to lie free on the sea floor. Presumably stimulated by contact with the chalky ooze, the mantle edges of the left

valve secreted a set of long tubular spines at the crests of the zigzag of that valve (i.e. in the *troughs* of the commissure if the shell is viewed in the life position). These spines (Pl. 85, fig. 4; Pl. 87, figs. 6, 7; text-fig. 6) extended at right angles to the shell outline, were sub-parallel to the plane of the commissure, and sometimes half as long as the shell itself. They were only secreted along the anterior arc of the commissure. Occasional specimens (e.g. SM B6461) that did not progress beyond the attached phase of ontogeny (stage 3 above) were able to utilize their anterior arc spines as additional 'roots' or 'props' to further stabilize their attachment. In these cases, of course, the spines were not sub-parallel to the plane of the commissure, but became irregular, and were generally directed downwards towards the surface of attachment.

5. In large, and presumably old specimens of *ricordeana* there was a slowing of the rate of introduction of new epithelial material in the generative arc, whilst over-all shell secretion continued. As a result extremely high vertical zones were built up. When this was the case, there was often secretion of further sets of spines around the commissure; on any one plica there may have been up to four successive spines, each vertically above (with respect to life orientation) its immediate predecessor (Pl. 86, fig. 3).

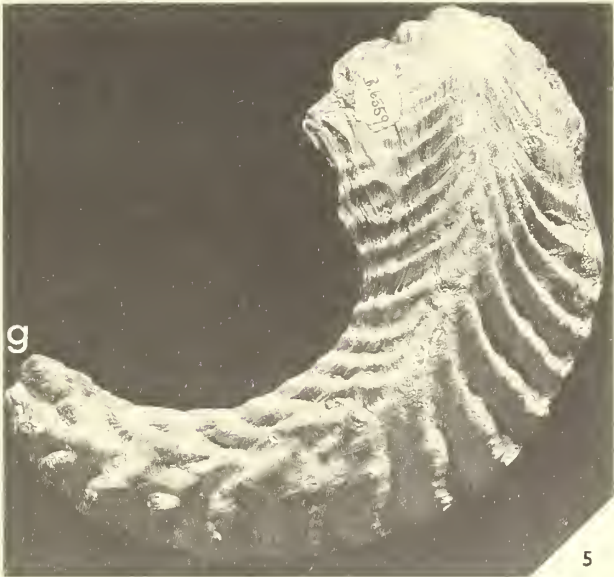
Other populations of colubrina

The long spines sub-parallel to the plane of the commissure, diagnostic of *A. colubrina ricordeana*, appear to be restricted to very local populations from particular horizons in the Cenomanian Chalk Marl of England and Normandy. However, populations of the *colubrina* group agreeing with *ricordeana* in all other aspects are common from rocks of Cretaceous age.

1. The Haslingfield population. A rich fauna of *Arctostrea* is known from the locality of Haslingfield, a few miles south of Cambridge. Specimens from this population (Pl. 85, fig. 5) are virtually indistinguishable from the Folkestone *ricordeana*, apart from their lack of long spines along the anterior arc. Occasionally broken spine stumps suggest that some specimens did secrete spines in this position, but the majority of the population possess very strong clumps of root spines proximally, and were clearly attached throughout their ontogeny.

EXPLANATION TO PLATE 85

- Fig. 1. *Arctostrea diluviana* (Linnaeus), Senonian, Essen, Germany. $\times 1$. Internal view of a typical upper (right) valve of this species; note the well-developed gill-gutter anterior to the adductor scar, with pustulose shell texture along its bottom. BM L61234.
- Fig. 2. *Arctostrea unguolata* (Schlotheim), Maastrichtian, Maastricht. $\times 2$. Internal view of an upper (right) valve to show the flat floor; note that the marginal zigzag is of amplitude equal to the depth of the valve. BM LL8600.
- Fig. 3. *Arctostrea unguolata* (Schlotheim), Upper Cretaceous, Buzi Valley, Portuguese East Africa. $\times 2$. This specimen shows well the characteristic flat-topped shell, and open crested plicae, that are so typical of the species group. BM L56928.
- Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. Approximately $\times \frac{1}{2}$. View of double valved specimen from below, looking up at the divaricating ornament and snowshoe spines of the under (left) valve. SM B.6451; specimen figured by Woods, text-fig. 122.
- Fig. 5. *Arctostrea colubrina* (Lamarck), Lower Chalk Marl, Haslingfield, Cambridgeshire. $\times 1$. A specimen showing the characteristic divaricating plicae and branchiform shape of the upper (right) valve when viewed from above. g, present position of the generative arc (growing edge) of the mantle margin; g', a previous position of the generative arc. SM B.6559.



CARTER, Functional morphology of *Arctostrea*

2. The Le Mans population. It was noted earlier that on the shell of an adult *Arctostrea* any given plica starts its history in the generative arc of the mantle edge as a small undulation in the growth-lines. In many populations of the *colubrina* group, for example, that from Cenomanian calcareous sandstones of Le Mans, this may develop next into a marked, short, tubular 'funnel spine' (Pl. 88, fig. 5), and only later grow into a sharp zigzag. The plica, of course, retains this funnel spine at its crest, and several more may be secreted in homologous positions as growth continues (Pl. 88, fig. 4). It is striking that these funnel spines are extremely well developed on the anterior margin, but are only rudimentary on the posterior (Pl. 86, fig. 2); they also tend to be rather better developed on the right (upper) valve.

THE *ARCTOSTREA UNGULATA* GROUP

Though the over-all shell morphology of *A. unguata* is similar to *A. colubrina*, there are significant differences in detail.

New plicae are again introduced distally in the generative arc, but the commissural zigzag is of much greater wavelength and amplitude than in *colubrina*. There is thus an apparent tendency for new plicae to be introduced in pairs on the anterior and posterior sides of the distal growing edge (Pl. 85, fig. 3). The zigzag also has broad, rounded extremities in contrast to the sharp, pointed extremities of *colubrina*.

The initial mantle edge reflection at the start of a new plicae (Pl. 85, fig. 3; Pl. 86, fig. 6) is broad and strong, and it retains a similar aspect throughout ontogeny. This, linked with the angle at which the mantle edge is held, results in the characteristic 'open-crested' plicae that typify the species. A similar open-crested morphology may be seen in the *A. pusilla* group (Pl. 90, fig. 9). The growth lines on the shell of *ungulata* beautifully display the early stage of differential mantle expansion, during which an initially gently undulose commissure is transformed into the broad, strong mantle reflection at the head of each plica (Pl. 86, fig. 6). However, after this initial stage of differential mantle expansion, further shell secretion results in the building up of a vertical zone in the usual fashion (Pl. 85, fig. 3).

It is likely that the differences in morphology between *colubrina* and *ungulata* are at least partly related to a difference in habitat, *ungulata* being usually collected from medium-grained or coarser calcareous sandstones, whilst *colubrina* is often common in finer grained sediments. The attachment scar is generally small and not well marked, and whilst some specimens may have been attached proximally throughout life, the majority probably lay free on the sea floor.

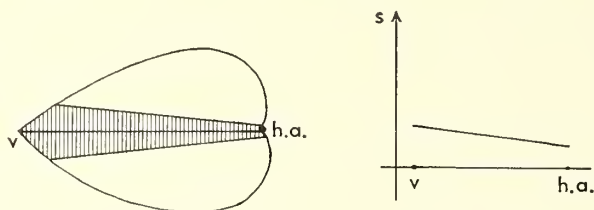
The *A. unguata* group is restricted to Upper Cretaceous rocks and has a wide distribution, ranging from Crimea, Bulgaria, and East Africa, as far north as Holland, Belgium, and Scandinavia. It seems to replace the *colubrina* group at this stratigraphic level. There is little doubt that *ungulata* developed from an attached species similar to *A. pusilla* (Nilsson) (see appendix).

THE *ARCTOSTREA DILUVIANA* GROUP

Members of this group have a larger and more solid shell than members of the previous two, this being a direct result of their being permanently cemented to the substrate throughout post-larval ontogeny.

It is characterized by its somewhat irregular, oval shape (Pl. 85, fig. 1) and its large size. Although there may be a zigzag all around the commissure, it is always best developed over the anterior margins, and it is only here that there is any vertical zone built up.

The *diluviana* group is in an Upper Cretaceous development, and seems to have a more limited distribution than *ungulata* or *colubrina*; specimens that I have examined all derive from northern Europe (Belgium, Holland, Germany, and Sweden).



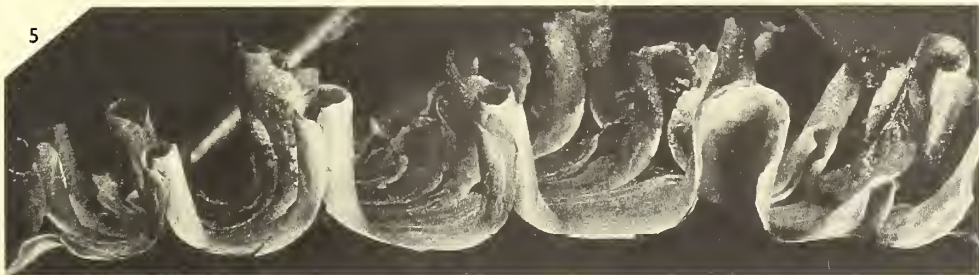
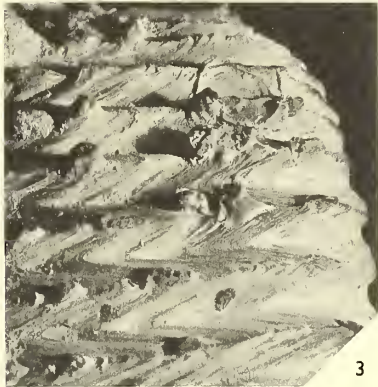
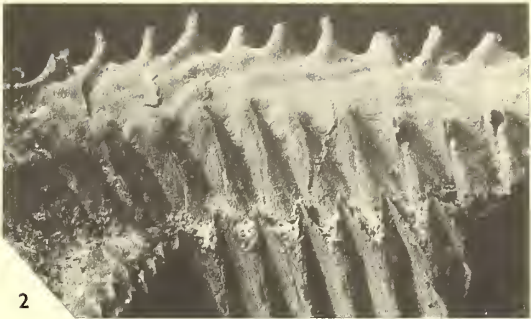
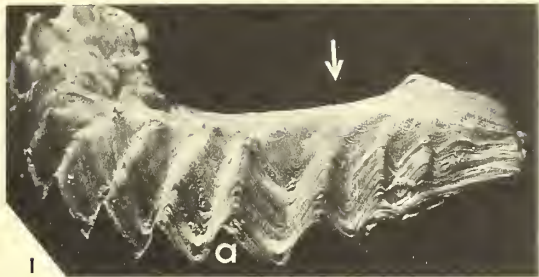
TEXT-FIG. 3. To illustrate the style of shell secretion in an equilateral bivalve; the growth increments (ruled area) on each valve are of wedge shape, tapering towards the hinge axis. *h.a.*, hinge axis; *v*, ventral margin; *s*, rate of secretion of shell material.

CONSIDERATIONS ON SHELL FORM

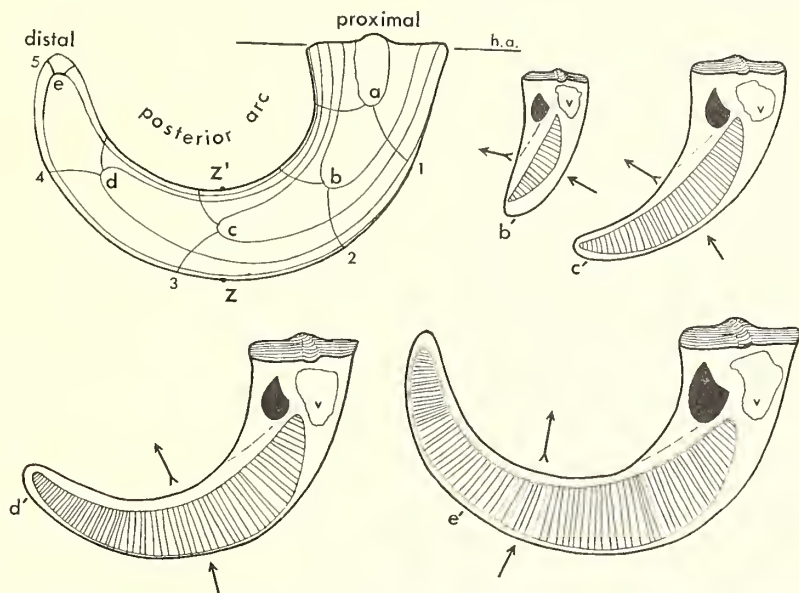
Fundamental tenets. Analysis of shell form in the Bivalvia becomes hopelessly confused unless a clear distinction is maintained between the basic phenomena of shell secretion *per se* on the one hand and generation of mantle cells (i.e. expansion of the area of mantle epithelium) on the other (Carter 1967). However, provided this distinction is maintained, it is possible to understand in detail the growth of even complex Bivalvia such as *Arctostrea*.

EXPLANATION OF PLATE 86

- Fig. 1. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. $\times 2$. Arrow marks the inception of plica 'a' in the generative arc; the shell is of a juvenile animal which had not secreted snowshoe spines at the time of its death. BM LL14751.
- Fig. 2. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Trouville, Normandy. $\times 2$. Note the development of funnel spines (more conspicuous on the anterior than on the posterior margins) in this view of the posterior vertical flank. BM 65748.
- Fig. 3. *Arctostrea colubrina ricordeana* (d'Orbigny), Chalk Marl, Norman Cement Works, Cambridge. $\times 1\frac{1}{2}$. View of part of the vertical zone developed on the anterior arc of the lower (left) valve, showing up to four broken snowshoe spine bases (one above the other) on individual plicae. SM B.6557.
- Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), same specimen as 1. $\times 4$. Note the suppression of the more dorsal plicae.
- Fig. 5. *Pinna rugosa* J. de C. Sowerby, Recent, unlocated. $\times 1\frac{1}{2}$. View of the ventral valve edge to show the funnel spines. Note how the earlier spines are sealed off by the secretion of a sheet of shell across their base. UMZC 2008 (Saul Collection).
- Fig. 6. *Arctostrea unguolata* (Schlotheim), same specimen as Plate 85, fig. 2. $\times 4$. View of the posterior arc, showing the characteristic open crested plicae and the high amplitude of the zigzag.
- Fig. 7. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. $\times 4$. Showing a plica whose growth lines display a zigzag that is starting to diminish in amplitude (3) after an initial increase from its inception in the generative arc (1) up to a point of maximal amplitude (2). Plica is situated on the posterior arc of the upper (right) valve. BM L.80734.



Practical implications. In a bivalve of simple equilateral form (e.g. *Glycymeris*), secretion of shell is at a maximum somewhere along the ventral margins, and decreases dorsally on either side of this around the lateral shell margins (text-fig. 3). By virtue of its most unusual pattern of mantle cell generation, *Arctostrea* (text-fig. 4) has its point of maximal shell secretion (Z) situated on the anterior arc of the shell, secretion diminishing at points around the commissure both distally and proximally to this; then there is a further



TEXT-FIG. 4. An idealized adult specimen of *Arctostrea* marking in selected growth-lines (a through to e) and plicae (1 through to 5). The growth stages corresponding to each growth-line are drawn separately as growth series b' to e'; adductor muscle, solid black; h.a., hinge axis; v, visceral mass; gill, ruled lines; arrow marks functional centre of the inhalent current stream bathing the gill; feathered arrow centre of exhalent stream. Note how this point migrates relatively in a distal direction during growth. Z: point of maximal amplitude of zigzag on the anterior arc of the commissure, diminishing antero-proximally and antero-distally. Z': point of maximal amplitude on the posterior arc of the commissure, diminishing postero-proximally and postero-distally. (It should be emphasized that growth-lines a to e and plicae 1 to 5 are only selected examples from the continuous series of growth-lines and plicae that occur on the shell surface; see also Pl. 85, fig. 5.)

maximum of secretion (Z', but note that secretion here is itself absolutely less than at Z) on the posterior arc, secretion diminishing both distally and proximally from this point as well.

A further point of interest may be mentioned here: the hinge axis in *Arctostrea* is situated at the proximal end of the shell, and hinging takes place by rotation about this axis (text-fig. 4). However, the extension of the axis itself has a limiting effect upon the adult shell form of the animal for, if efficient hinging is to be maintained, it is impossible for the distal growing edge of the shell to transgress over the extension of the hinge axis. Individual specimens of *Arctostrea* show many modifications in late adult life to cope with this restriction, two of the commonest of which can be seen on text-fig. 1. Fig. 1e shows an individual that has solved the problem by increasing the curvature of its

growing edge so as to grow directly back towards the umbones—extreme specimens may actually fuse their shell into a complete ‘circle’. Fig. 1f shows the other alternative, where the growing edge is directed away from the umbones.

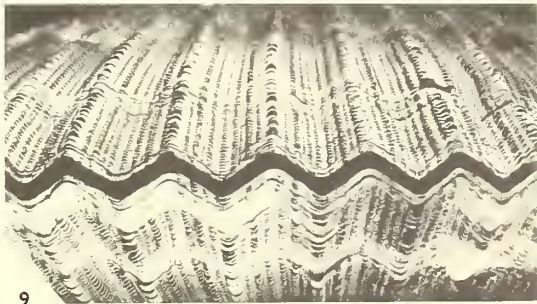
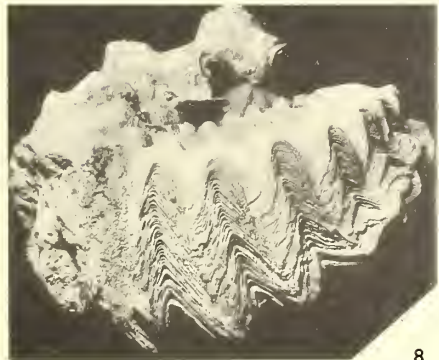
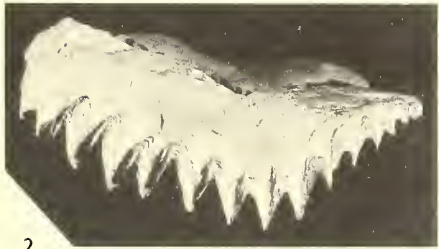
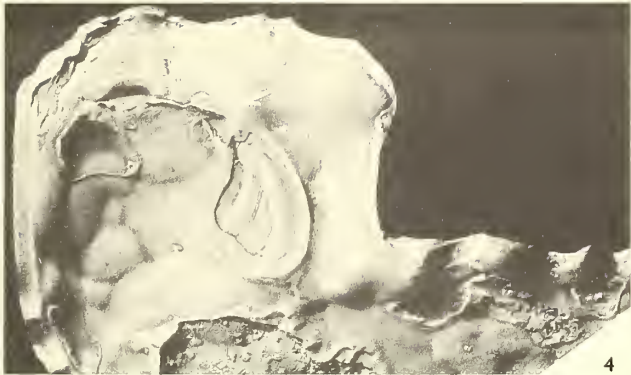
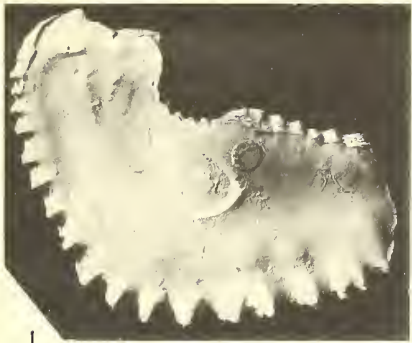
Consequences of cementation. Populations of *Arctostrea* convincingly demonstrate the close relation that exists between shell cementation and irregularity of form; the greatest regularity of adult shape is always found in those members of the *colubrina* and *ungulata* groups that were unattached during the major part of their adult life (Pl. 85, fig. 4). However, all extremes of variation can be found throughout the Jurassic and Cretaceous, from specimens that are cemented throughout life, and hence have a morphology mimicking the ‘*diluviana* group style’ (even though they may actually be *ungulata* or *colubrina* group), to specimens that are briefly cemented but break free early in adult life; these may be said to have a ‘*colubrina* group style’. It is possible to find specimens approaching these two morphological end members from a single population at almost any locality possessing *Arctostrea* in abundance. It is small wonder, in the light of this, that the systematics of the group is burdened by a plethora of unnecessary names; nor is there any hope of substantial improvement until the adaptive significance of these morphological trends is understood.

In oysters that remain attached throughout ontogeny by a considerable portion of their left valve, the shape of the left valve is mainly dependant upon the form of the surface to which the oyster is attached; in turn, the shape of the right valve is influenced by the fact that its edge everywhere has to meet that of the left. Consequently the form of the whole animal is strongly influenced by the shape of the substrate to which it is cemented. This is clearly demonstrated in the specimens of *A. pusilla* figured on Pl. 90, figs. 3–4, 6–10.

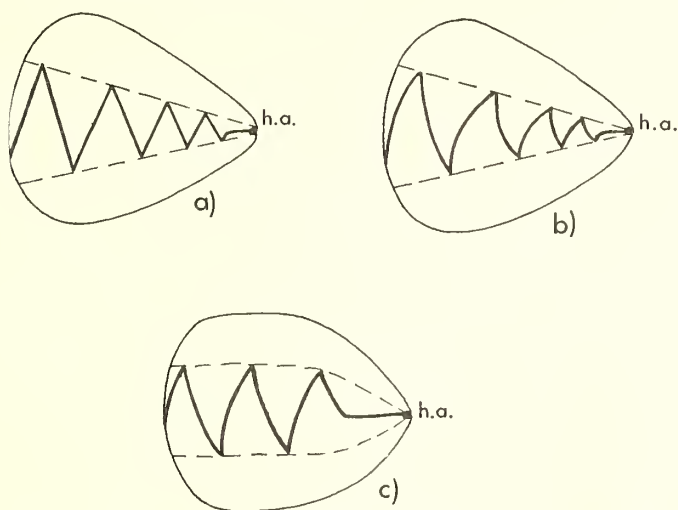
All adult *Arctostrea* have a sharply zigzag valve edge. Assuming that the shell is cemented to a reasonably flat surface, it is, of course, only possible for the animals to

EXPLANATION OF PLATE 87

- Figs. 1, 2, and 3. *Arctostrea alaeformis* (S. Woodward), Upper Chalk, Norwich. $\times 1$. Internal, ventral and external views of the lectotype. NCM F.C.2100; specimen of Woodward 1833, plate 6, fig. 3.
- Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. $\times 2$. Internal view of the upper (right) valve. Note especially the lack of room for a promyal passage dorsal to the adductor (arrow); and the characteristic pustulose nature of the shell on the floor of the valve. SM B.6462.
- Fig. 5. *Arctostrea pusilla* (Nilsson), Upper Chalk, Norwich. $\times 2$. A specimen with the more usual open textured plicae along the lateral margins, but with large open folds of the ‘*larva*’ type along the distal margins. View looking into the generative arc. NCM. F.C.2129a; specimen figured by Woods, plate 58, fig. 2.
- Fig. 6. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. $\times 4$. Specimen showing a funnel spine located at the top of a plica (arrow). In the adult growth stage, the same plica is the site of secretion of a snowshoe spine, subparallel to the plane of the commissure. SM B.6459.
- Fig. 7. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. $\times 2$. Typical development of short snowshoe spines in a specimen of only moderate overall size. SM B.6451; specimen figured by Woods, text-fig. 122.
- Fig. 8. *Arctostrea ungulata* (Schlothheim), same specimen as Plate 85, fig. 3. $\times 1$. View from antero-dorsal aspect.
- Fig. 9. *Chlanys asperimus* (Lamarck), Recent, Tasmania. $\times 2$. Note the presence of a true zigzag commissure (and not merely an interlocking valve edge) of low amplitude; this is one of the very few examples of this feature in the Bivalvia outside of the Ostreacea. SM D.20869.



produce a regularly zigzagged valve edge if shell secretion has been such that after a particular stage in ontogeny the growing edge of the shell is *not in contact with the substrate*. This may be accomplished in one of two ways: either the rate of mantle expansion is such that the shell soon comes to grow outside the edge of the object to which it is attached, which hence must be relatively small; or, if the attachment object is large, there must be a cessation of mantle cell generation during continued shell secretion, resulting in the formation of a marginal 'vertical zone'. The former is the dominant solution utilized by members of the *colubrina* and *ungulata* species groups; the latter by the *diluviana* species group. In either case, adult animals possess a regular and very sharply zigzagged commissure, the form of which is entirely independent of the form of the animal's attachment surface.



TEXT-FIG. 5. Theoretical types of zigzag commissure. (a) zigzag with diminution of amplitude dorsally, but with straight flanks; efficient hinging of the shell is impossible; (b) a geometrically graded zigzag, with both diminution of amplitude dorsally, and curved flanks to enable unimpeded opening and closing of the shell; (c) zigzag without diminution of amplitude dorsally; note that such a zigzag cannot reasonably cover any length of the lateral shell margins, and that it involves a non-linear secretion gradient across the shell.

The problem of grading. Interesting questions are raised by the interaction of the secretion pattern of *Arctostrea* with its possession of a zigzag commissure.

In a closely reasoned analysis of zigzag commissures in the Brachiopoda, Rudwick (1964) has introduced the concept of a *graded zigzag slit*, which is defined as a slit 'of uniform width all round the commissure, from one suppression point [the point where the zigzag dies away to nothing on the lateral shell margins] to the other'.

It is useful to isolate the morphological components that go to make up a graded zigzag slit:

1. Diminution. For a zigzag slit that occupies any appreciable length of the whole commissure there is a gradual diminution of amplitude of the zigzag as the hinge axis is approached (text-fig. 5a). This is inevitable if a linear secretion pattern is to be

maintained across the shell, though it is, of course, possible to imagine a shell form in which the zigzag does not diminish in amplitude dorsally and hence does not possess a linear secretion pattern (text-fig. 5c).

2. Curvature of the flanks. As Rudwick has already clearly pointed out (1964), by virtue of the hinging motion of any bivalved shell, it is impossible for a zigzag situated on the lateral margins to have straight flanks. Such a shell (text-fig. 5a) would be unable to open because of the occlusion of the shell edges in the crests and troughs of the zigzag. It is therefore necessary that the flanks of the zigzag be curved, concave dorsally, in order to overcome this occlusion (text-fig. 5b). An inevitable *result* of such flank curvature is that there is a tendency to equalization of width of the slit.

Rudwick is of the opinion that the actual flank curvature is due 'partly to the . . . (requirements) . . . of a slit of uniform width, and partly to the fact that the valve edges move apart by rotation'. In other words, he suggests that there was a positive selective value in favour of a slit of uniform width during the evolution of zigzag slits, and that their flank curvature cannot be explained on a basis of shell secretion tenets alone.

Whilst this may be the case in the Brachiopoda, within the limits of accuracy of the measurements it is possible to make, it appears that the curvature of the flanks of the zigzag in species of *Arctostrea* is no more than is necessary to ensure the adequate hinging of the shell. An inevitable result of this is a slit of roughly equal width all round the commissure, but economy of hypothesis precludes treating this equality of width as of prime selective significance. As the term 'grading' is of considerable usefulness in morphological description, it is necessary to distinguish 'adaptive grading' where the equalizing of the width of the slit is thought to have adaptive significance over and above that concerned with shell hinging (i.e. grading *sensu* Rudwick), from 'geometric grading', where all elements of the grading, including both diminution of amplitude and curvature of the zigzag flanks, are thought to be explicable in terms of basic tenets of shell secretion.

EXPLANATION OF PLATE 88

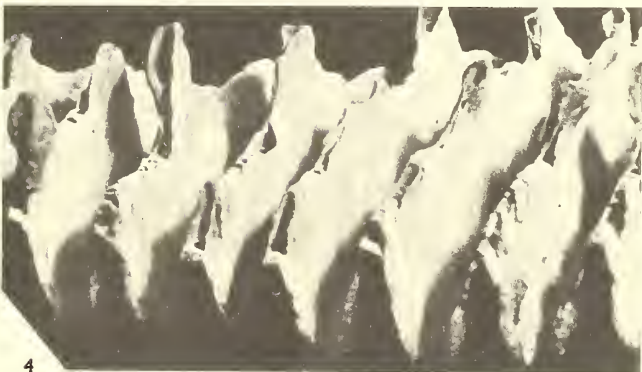
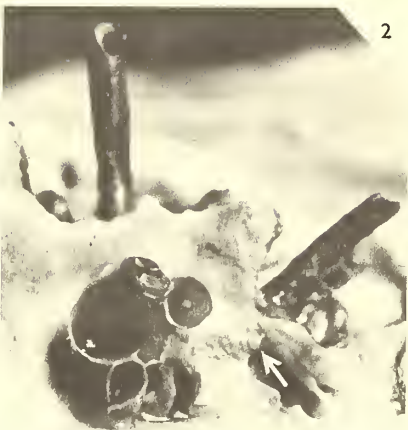
Fig. 1. *Etheria elliptica* Lamarck, Recent, Africa. $\times 1$. Well developed funnel spines at spaced intervals around the edge of the commissure. These spines must be secreted by reflected lobes of mantle tissue, and are sealed off as soon as they are no longer right at the growing edge of the shell. UMZC 2000 (McAndrew Collection).

Fig. 2. *Crassostrea echinata* (Quoy and Gaimard), Recent, Australia. $\times 6$. A juvenile shell (umbo arrowed) showing the extreme development of flaring, funnel spines on the ventral side of the shell. The long, thin funnel spines of a slightly later growth stage can be seen out of focus in the background. UMZC 2007.

Fig. 3. *Arctostrea colubrina* (Lamarck), Lower Chalk, Cherry Hinton, Cambridgeshire. $\times 1$. Note the presence of two folds (arrowed) on the posterior ear; these probably reflect the presence of persistent pseudo-siphons in the mantle edge. SM B.358; figured by Woods, text-fig. 135, and Rudwick (1964), plate 29, fig. 5.

Fig. 4. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Le Mans, Normandy. $\times 7$. A specimen exhibiting the successive secretion of several funnel spines on individual plicae; note the very low amplitude of the zigzag. BM LL26833.

Fig. 5. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Le Mans. $\times 7$. View of the generative arc (distal end) of the right valve of a young individual. Note the sharp commissural zigzag with funnel spines developed at the crests. BM LL26832.



The uniqueness of individual specimens. The shell of any specimen of *A. colubrina* has a unique morphological construction, yet its secretion was none the less governed by certain basic conditions:

1. The vast majority of new epithelial cells were introduced in a narrow generative arc of the mantle edge.
2. The absolute secretion of shell material was a function of distance from the hinge axis, being maximal at the point on the commissure furthest from the hinge axis.
3. After a certain growth stage had been passed, the shell possessed a zigzag commissure; at all further growth stages this was geometrically graded in such a way as to ensure the free hinging of the shell and the tight approximation of the valve edges when shut.

The consequence of these conditions is that *every single plica* on the shell of a typical *Arctostrea* has a morphologically unique ontogeny.

Considering (for convenience only) the hinge axis as a fixed direction, it is apparent that the generative arc of the mantle edge occupies a geometrically unique position for every successive commissure throughout the life of the animal (text-fig. 4, positions *a* through to *e*). Since the generative arc is the site of inception of all new plicae, each plica starts its ontogeny in a geometrically unique position, and its detailed structure is a reflection of its exact positions on either the anterior or posterior margins.

These detailed structural changes are mirrored on the valve surface in the form of growth-lines (Pl. 86, figs. 1, 7). A study of these reveals that the earlier formed plicae (e.g. plica 1 of text-fig. 4) pass through a series of growth stages which may be idealized for conceptual convenience. This series generally follows the pattern illustrated by the plica of Pl. 86, fig. 7.

Initially the amplitude of the zigzag is small, corresponding to its inception on the generative arc of the commissure (position 1 of Pl. 86, fig. 7), but this rapidly increases towards a maximum. Meanwhile, further mantle expansion has been taking place distally (in the generative arc), causing the relative migration of the zigzag around the commissure in a proximal direction. The amplitude of the zigzag reaches a maximum (position 2 of Pl. 86, fig. 7), and then starts to come under the influence of the diminution of amplitude along the antero-proximal part of the commissure; it hence decreases in amplitude (position 3 of Pl. 86, fig. 7). On the very earliest formed plicae (e.g. plica 1 of text-fig. 4; Pl. 86, fig. 4) this decrease in amplitude may be carried as far as total suppression of the zigzag.

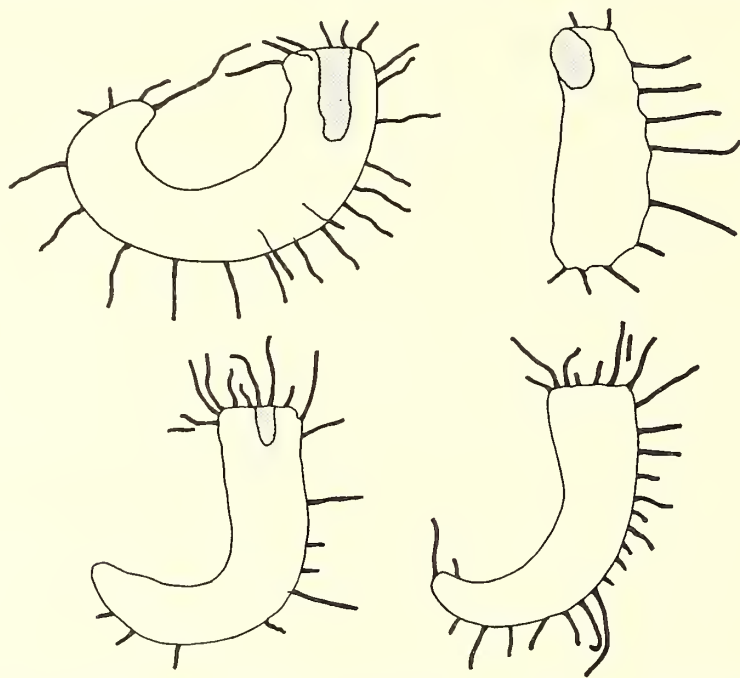
THE FUNCTIONAL INTERPRETATION OF *ARCTOSTREA*

Plicae. Viewed from above, the shape of an adult *Arctostrea* is crescentic (text-fig. 1; Pl. 85, fig. 5); it is immediately obvious that the inner arc of the crescent (i.e. the posterior margin) is shorter than the outer arc of the crescent (the anterior margin). It follows that for a zigzag of given wavelength, on any given commissure there are fewer zigzags (and therefore plicae) on the posterior margin than on the anterior. The more sharply crescentic is the over-all shell shape, then the fewer plicae there are posteriorly compared with anteriorly. For example, on a fairly sharply recurved specimen (SM B.6557) there are 13 posterior plicae, and 19 anterior plicae. There is no need to seek

a functional interpretation of this fact; it is an inevitable consequence of the mode of growth.

Spines. There are three different types of spine on *A. colubrina ricordeana*, and it is possible to attribute to each a discrete functional role:

(a) Attachment spines. It is self-evident that the complex of spines secreted at the proximal end of the shell around the attachment area served to strengthen the attachment of the shell to the substrate. Their restriction to this part of the shell, their irregular



TEXT-FIG. 6. Shell outlines of *Arctostrea colubrina ricordeana* to show the disposition of spines on the left valve with respect to the over-all shape of the shell; specimens viewed from above. Note especially their concentration around the umbonal end of the shell (attachment spines), and their disposition at right angles to the shell margins (snowshoe spines). Stippling as for text-fig. 1; specimen without stippling is a left valve only. $\times \frac{1}{2}$. All specimens from the grey Chalk Marl, Folkestone, Kent.

BM L4855.

and intertwined shape, and the fact that they are occasionally preserved attached to hard objects such as other oysters, all support such an interpretation.

(b) Snowshoe spines. Similarly, it was self-evident to Woods over fifty years ago that 'the long regular outgrowths from the margin of the valves occur [only] in specimens from the Chalk Marl, and were no doubt adopted for the purpose of fixation in the soft sediment of the sea floor', but it is worth noting how closely the observed morphology of the spines approaches the paradigm for a 'snowshoe' function. By virtue of its arcuate shell shape, the distal and proximal ends of the shell in an adult *colubrina*

morphologically define one 'side' of the shell, whilst the curved anterior margin defines the other (text-fig. 6). Most of the weight of the shell is concentrated on the anterior margins, and it is clearly there that the animal was in most danger of sinking into the substrate. Hence it is there that the spines are developed, one at the trough of every zigzag. Their length, their sub-parallelism to the plane of the commissure, their disposition at right angles to the shell outline, and the successive secretion of more than one spine on individual plicae in large adults with high vertical zones (Pl. 86, fig. 3), all add up to unequivocal evidence that the spines prevented the animal from being smothered by sinking into the soft ooze.

(c) Funnel spines. The function of the small funnel-like spines, developed at the crest of the zigzags on the right (upper) valve, will be discussed in a later section on the function of the zigzag itself.

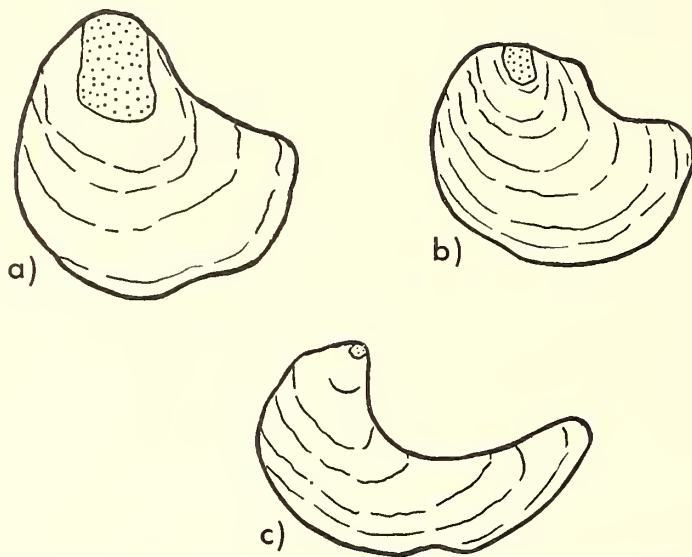
The arcuate shape. From the very early stages of ontogeny of *Arctostrea*, the localized generation of epithelial material in the generative arc of the mantle edge exercised a controlling influence on the shell form; it is directly responsible for the characteristic arcuate shape in plan view. This arcuate shape approaches a logarithmic spiral, since the shell always tends to grow in such a way as to preserve over-all similarity of shape.

However, the tendency of oyster shells to arcuate shape is by no means confined to *Arctostrea*, and Lang (1923) has coined the term *lunate* to describe it. Functional explanations are not common; most writers seem content to follow the suggestion of Douvillé (1910) that this shape of shell is ideally suited to resist water currents. At its best this postulate is difficult to understand; and the fact that a lunate trend can be recognized so frequently in groups of oysters at such different points in time and space (e.g. *Liostrea anabarensis* Bodyl from the Valanginian of Russia (text-fig. 7); *Crassostrea ameghinoi rocana* von Ihering from the Danian of Argentina (text-fig. 8); and the Recent *Crassostrea angulata* (Lamarck)) leads one to be dissatisfied with Douvillé's explanation and to suspect that some basic adaptation is involved.

The soft-part anatomy of *Ostrea edulis* (text-fig. 9) is fairly characteristic of the Ostreacea as a whole, and most members of the Pectinacea have a grossly similar anatomy. This anatomical similarity is undoubtedly a result of their mode of life *on* the substrate with the commissure horizontal, possessing the ability to take in water (and hence food) over a large part of their commissure. Many bivalves that live with their commissure at right angles to the substrate (e.g. *Arca*) have gills which hang vertically in the mantle cavity, and which are not fused laterally to the general mantle surface. Generally speaking, however, the assumption of a horizontal mode of life necessitates the lateral fusion of the gills (particularly the upper) with the mantle surface; otherwise gravity would cause them to fold together in a most inefficient way. It is thus perhaps significant that the advanced pseudo lamellibranch gill condition is characteristic of the Ostreidae, Pectinidae, and Pteriacea—all groups which live with the commissure sub-parallel to the substrate.

The presence of an inhalent current along a considerable part of the commissure requires the development of larger and more complex organs to catch, sort, and process the available food supply. The Pectinacea and Ostreacea have dealt with this requirement by enlarging the gill and expanding it into a characteristic crescentiform organ fitting snugly between the major adductor muscle and the free valve margins. A

comparison of the shape of the gill of a typical pectinid and ostreid with the shell shape of 'lunate' oyster species (text-fig. 1) can leave no doubt that this lunate shape is a direct reflection of the size and importance of the gill in fossil species such as *A. colubrina*. This organ was of such paramount importance to these fossil species that it assumed a dominance over all other soft parts.



TEXT-FIG. 7. A lineage of oysters from the Upper Jurassic and Lower Cretaceous of Siberia that exhibits a continuous trend towards branchiform shape; notice the concurrent reduction in size of the attachment scar (stippled). (a) *Liostrea* ex. gr. *delta* (Smith), Kimmeridgian; (b) *Liostrea praeanaabarensis* Zakharov, Volgian; (c) *Liostrea anabarensis* Bodyl, Valanginian. All $\times \frac{1}{3}$ (after Zakharov 1965, fig. 1a, c, and i).

The gill of Recent bivalves, including oysters, grows by the addition of filaments to its distal end (Yonge 1960). This corresponds exactly with the position of the 'generative arc' in fossil *Arctostrea*; as the gill grows by distal addition of new filaments, so must the shell have been expanded in a similar direction in order to provide protection for the growing gill. Examination of Recent oysters (e.g. *Pycnodonte hyotis* (Linnaeus)) in which the *over-all* shell shape is not arcuate, reveals the presence on the floor of the valves, particularly the left, of a marked arcuate gutter in which the gill is situated. There is a similar 'gill gutter' in many fossil species (e.g. *Arctostrea diluviana* (Linnaeus), Pl. 85, fig. 1). In both fossil and Recent species the floor of this gutter is often lined with shell of a peculiar pustulose character; in specimens of *Arctostrea* similar pustulose structure can be observed along the length of the shell (Pl. 87, fig. 4).

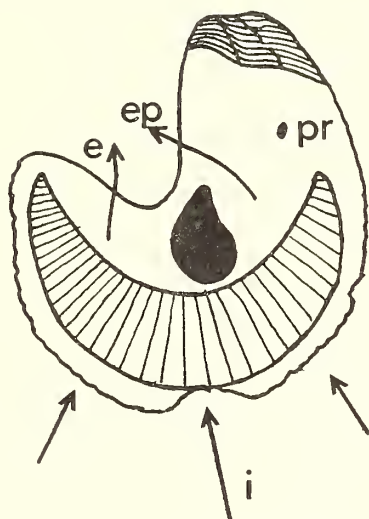
In view of the close functional relationship between the gill and shell shape, the term *branchiform* will be used to describe species that reflect this relationship in their external shell form.

Sanitation. Sanitation is a general problem that arises amongst animals that have adopted a horizontal mode of life on the sea floor. In the Bivalvia it is usually effected

by the accumulation of pseudofaeces around the edge of the mantle cavity, and their periodic ejection by sharp contractions of the adductor, but such a mechanism may be insufficient in turbid waters. It appears to be accepted amongst writers on Recent oysters (e.g. Menzel 1955) that the presence of a promyal chamber in Recent *Crassostrea* is a specific adaptation to allow a greater flow of water through the shell, and hence to aid with sanitation and to prevent the exhalent chamber from being invaded by sediment. (The promyal chamber (present in the right valve only) is an additional passage for the exhalent current situated *dorsal* to the adductor muscle; it is formed by the local separation of the mantle from the underlying body-tissues.)

Certain extinct oysters certainly possessed promyal chambers. For instance, the Danian *Crassostrea ameghinoi rocana* has an adductor scar situated distant from the dorsal margin (text-fig. 8), a sure sign of the promyal chamber in Recent species. In addition there is a conspicuous pedal retractor scar in this species, suggesting that the foot was an active aid to mantle cavity cleansing.

However, the morphology of *Arctostrea* is such that we can be equally certain that it lacked a promyal chamber. The adductor scar is generally very close to the dorsal margin, and there is no room at all for an efficient flow of water dorsal to it (Pl. 87, fig. 4). Yet the most branchiform specimens of *Arctostrea* in the Jurassic and Cretaceous are found in fine-grained muddy sediments such as the Oxford and Kimmeridge Clay, and the Chalk. It is in just that type of environment that efficient water circulatory and cleansing mechanisms are of paramount importance; in the absence of a promyal chamber it must be assumed that the large size of the gill itself was adaptive in this respect, since it would ensure a very powerful current of water through the branchiform shell.



TEXT-FIG. 8. *Crassostrea ameghinoi rocana* von Ihering, Danian, Argentine. $\times 1$. Reconstruction of the gill and feeding currents. *I*, inhalent current; *E*, exhalent through current; *EP*, exhalent current from promyal chamber; *PR*, pedal retractor muscle; adductor in solid black; gill, ruled lines. BM LL26838.

The zigzag commissure. Rudwick (1964) concluded that in the Brachiopoda zigzag commissures serve two purposes, both fundamentally protective: firstly, for any given gape a zigzag prevents the entry of particles above a certain size, whilst conferring a relative increase in the area of slit actually functioning as intake; secondly, since the mantle tissue lining a zigzag slit is sensitive, there is also a relatively larger amount of sensitive warning tissue available to the animal in proximity to its shell edge.

One would expect it to be significant that the only Bivalvia that possess plicate commissures homoeomorphic with the brachiopods are those that have adopted the brachiopod mode of life and ecologic niche. Whatever the significance of zigzag commissures might be, one would *a priori* expect it to be similar in the two groups. Yet it does not seem to me that Rudwick's explanation is applicable to *Arctostrea*.

The first of the above postulates is unsatisfactory on two counts. Firstly, *Arctostrea* lives dominantly in finer-grained sediments, generally of or below sand grade; I know of only one locality where it is collected associated with small pebbles. Secondly, and more seriously, bivalves do not remain feeding whilst being pelted with a miniature hailstorm of sediment, no matter how paradigmatically rigorous their zigzag commissures may be. In conditions of high turbidity, the average bivalve firmly closes its shell. It is fair to conclude that *Arctostrea*, when inhabiting its usual facies, would have had its valves gaping more widely than the average size of particles present in the substrate and therefore that the zigzag commissure would have offered virtually no protection at all against ingestion of such material.

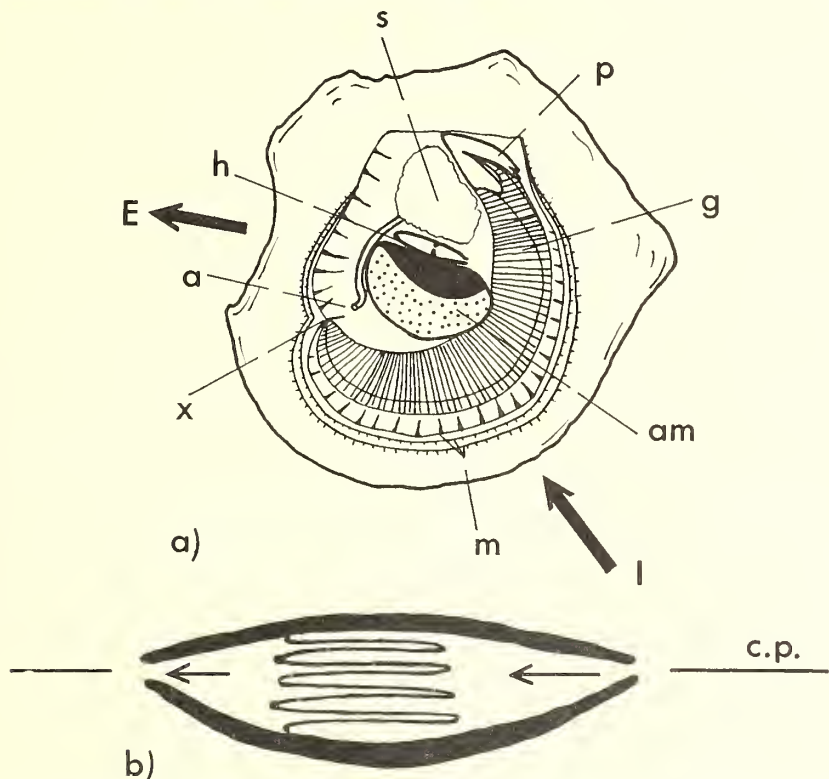
The second of the postulated functions has the same structural paradigm as the first (one of the problems of mechanistic analyses is that differing functional interpretations can have very similar structural paradigms), and there is little that can be added to Rudwick's original discussion. Undoubtedly, given that the mantle edges are sensitive to clouds of (say) silt, and will cause the shell to close on contact with such a cloud, then a zigzag commissure is relatively more efficient than a similarly long planar commissure. But whether this gain in efficiency is sufficient to explain the evolution of a zigzag slit is open to some doubt, particularly as this interpretation fails to account for one of the more striking features of the morphology of *Arctostrea*—that the zigzag is conspicuously just as well developed over the *exhalent* posterior borders as it is over the *inhalent* anterior borders (Pl. 86, figs. 2, 6, 7). (This was not as marked a feature of the earlier Jurassic members of the group, where the zigzag is noticeably not as well developed over the exhalent as over the inhalent currents.)

Assuming that the zigzag is a significant feature of the morphology, how then is it to be interpreted? It would not seem likely that the zigzag was for the purpose of preventing anything from leaving the shell. We are left with two alternatives:

1. The zigzag was physically preventive against the entry of harmful agents. We have already concluded that it is unsatisfactory to believe that the zigzag slit served to keep out large 'ball-bearing' type particles, particularly since it is equally developed all round the shell. The implication is that, if the zigzag was to prevent the entry into the shell of some harmful agent or other, then this agent must have been capable of penetrating against the powerful exhalent stream of the oyster. This immediately precludes sediment and suggests a motile, and hence organic, agent. Thus it might be considered that the zigzag served to prevent the penetration of small irritants such as crustacea and fish into the mantle cavity (M. J. S. Rudwick, personal communication). Whilst this is a function which a zigzag commissure must inevitably fulfil by nature of its morphology, it is open to some doubt whether or not this is an explanation that can explain the evolution of the zigzag.

2. The zigzag had a beneficial hydrodynamic effect on feeding currents. A zigzag slit has an inevitable hydrodynamic effect on the water flowing through it. First, and most important, due to the geometry of the zigzags there is an effective vertical spatial spread of the inhalent and exhalent currents; this is so whether the current was an external one or was merely the feeding current intrinsically generated by the oyster itself. Accompanying this, there would probably be a tendency for jet streams to form at the crests and troughs of the zigzags; any such tendency would be of considerable value, particularly on the exhalent margin where it would assist in carrying ejected sediment away from the

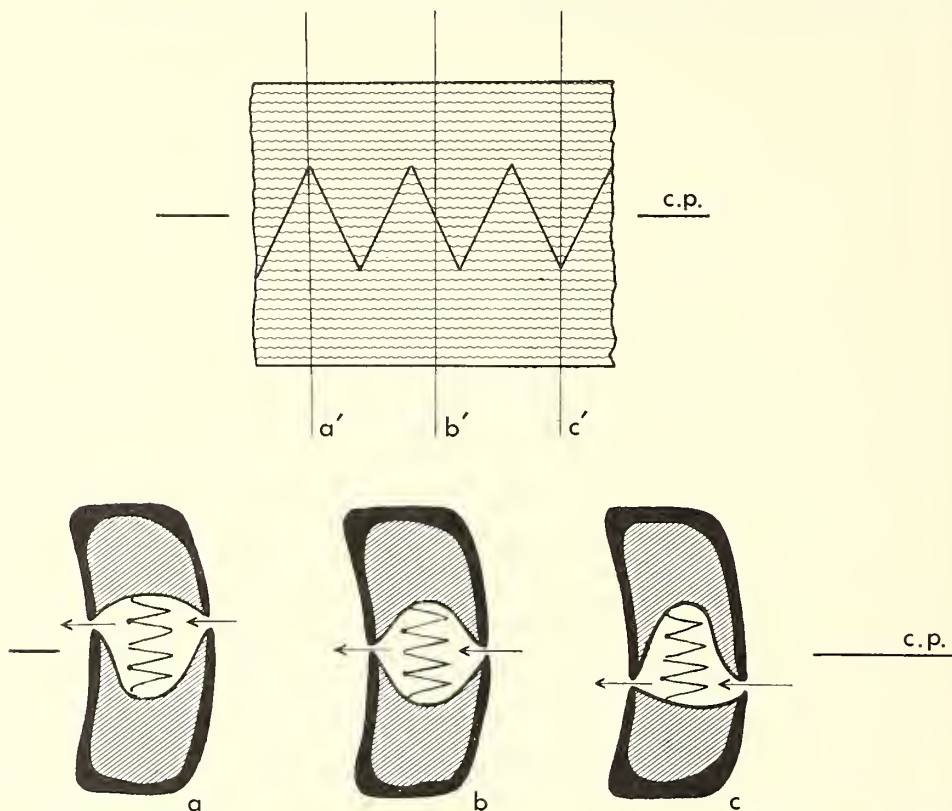
edge of the shell (cf. the exhalent gill streams of the Lamprey). It must also be remembered that it is not only the topology of the shell edges that affects the inhalent current stream of a feeding oyster. In all Recent oysters the muscular flexibility of the actual mantle edges is an important factor influencing the direction and strength of feeding currents. By approximating its mantle edges along the flanks of the zigzag, but leaving them parted at the crests and troughs, *Arctostrea* could have greatly enhanced any natural tendency for jets to form at these points.



TEXT-FIG. 9. (a) Soft part anatomy of *Ostrea edulis* Linnaeus (after Yonge 1960). *p*, palps; *g*, gill; *am*, adductor muscle; *m*, mantle edge; *x*, distal point of junction of the gill and mantle lobes; *a*, anus; *h*, heart; *s*, visceral mass. *I*, inhalent current stream; *E*, exhalent current stream. (b) Diagrammatic cross-section through the mantle cavity and gills of *Ostrea edulis*, with feeding currents indicated by arrows. *c.p.*, plane of the commissure.

The pseudolamellibranch gill of an oyster is roughly W-shaped in cross-section, each V corresponding to a demibranch (text-fig. 9*b*). There are two such gills, which are attached to the mantle surface marginally and distally, and thus effectively partition the mantle cavity into two chambers and act as a 'sieve-strainer' to the inhalent current stream. In a typical oyster the gills are fairly close together and form thin high Ws (text-fig. 9*b*). Since the lateral cilia on each filament draw the water through the gill at right angles to the gill lamellae, the general inhalent current stream is impinging on the gill lamellae at a very oblique angle and filtering is somewhat inefficient. Obviously more efficient feeding, and in particular a higher rate of water filtration, will be possible if the gill-W becomes wider, for this would ensure that the current stream impinges on

the individual gill lamellae at a high angle (text-fig. 10). Of course, in order for this adaptation to be possible, the animal first has to have evolved a deeper body cavity. However, given such a deeper body cavity, feeding would obviously still be relatively inefficient if the commissure were to remain planar, for the inhalent current would not spread laterally far enough to meet directly the majority of the gill surface. But should the valve edge become plicate, then these problems are solved at a single stroke: the



TEXT-FIG. 10. Reconstructed cross-sections through the gill and mantle cavity of *Arctostrea*. (*a-a'*) an inhalent current entering the shell at the crest of a zigzag is best situated to bathe the upper gill; (*b-b'*) an inhalent current entering medially on the flank of a zigzag is best situated to bathe the inner demibranchs of both gills; (*c-c'*) an inhalent current entering at the trough of a zigzag is best situated to bathe the lower gill. *c.p.*, theoretical plane of the commissure.

gill-W can become relatively wider and still be bathed directly in strong inhalent current streams. The effect of a zigzag slit such as that of Pl. 86, fig. 6, *must* be to effectively separate the inhalent current into a set of streams (at the crests of the zigzags) for the upper gill, and a set of streams (at the troughs of the zigzags) for the lower gill. And since it is equally important that there be efficient exhalent current streams the zigzag is developed over the exhalent length of the commissure as well. Phylogenetically one would expect the inhalent zigzag to be the first to be selected for, which is just what is observed in primitive populations of *Arctostrea*.

Further comments on diminution. It was earlier noted (p. 468) that it is theoretically

possible to construct a shell in which the zigzag does not diminish in amplitude along the lateral flanks, but only by assuming that the secretion pattern across such a shell be non-linear (text-fig. 5c). In view of the almost axiomatic presence of linear secretion patterns in the Bivalvia (this contrasts with their common absence in the Brachiopoda), it is possible to argue that no specific functional (or adaptive) significance be attributed to diminution of amplitude of a zigzag on the lateral shell margins, for such diminution is an inevitable result of a linear secretion rate. By terming the zigzag commissure of *Arctostrea* a 'geometrically graded' zigzag, I have aligned myself with this view. However, should it be felt that a more strictly adaptive explanation is necessary in order to satisfactorily account for the diminution of zigzag amplitude, the interpretation given above for the over-all shell shape and initial presence of the zigzag (that they are linked with the size and importance of the gills) may also be applied here.

Several writers (e.g. Yonge 1926) have noted that in Recent *Ostrea* the inhalent current is strongest in the middle of the gill, and falls off considerably to either side of the mid-point (cf. text-fig. 9). The diminution of amplitude of zigzag in *Arctostrea* is such that it occurs towards the two ends of the gills, thus automatically ensuring that the inhalent current be relatively weaker here than in the centre of the gills. Obviously, though a shell such as text-fig. 5c is theoretically possible, such a zigzag would furnish undesirably strong inhalent currents right at the ends of the gills. It may also be noted here that the complete suppression of the more dorsal zigzags on the commissure of *Arctostrea* (cf. Pl. 86, fig. 4) only takes place after the zigzags in question have migrated relatively dorsal of the functional end of the gill (Plica 1, text-fig. 4).

Zigzag commissures in other bivalve genera. The presence of a true zigzag commissure is rare in the Bivalvia; the only other occurrence known to me is in the Australian pectinid *Chlanys asperrimus* (Lamarck) where a sharp zigzag of low amplitude and relatively constant wavelength can be seen (Pl. 87, fig. 9). It seems probable that zigzags are related to the demands made by inhalent currents spread round most of the commissure, and hence are restricted to bivalves that live lying on the substrate with their commissures horizontal.

Funnel spines

1. *Arctostrea*. Granted that the zigzag valve edge has the functional significance attributed to it above, we have an important clue as to the function of the small 'funnel spines' of *Arctostrea*. It will be remembered that these spines are invariably developed at the crests of plicae on the anterior valve margins but are usually poorly developed over the posterior valve margins (cf. Pl. 86, fig. 2; Pl. 88, fig. 5). Thus they are concentrated over the inhalent arc of the commissure and are only developed during that part of the ontogeny of a plica before the true zigzag of the plica has fully developed. It would, therefore, seem likely that they serve the same function as the zigzag itself does later; in other words they enable all parts of the gills to be irrigated with currents of water impinging as far laterally as possible. It is worthy of further note that those few populations that habitually secrete several of these funnel spines on a single plica, one beneath the other (Pl. 88, fig. 4), are just those populations that have a zigzag of conspicuously small amplitude.

It should be stressed at this point that though the above discussion has attributed a function to the shell spines themselves, it is, of course, flaring funnels of epithelium

along the mantle edge that have the primary functional significance as far as inhalent current streams are concerned; the actual funnel spines on the shell are doubtless secreted partly as support, and partly as protection for such epithelial funnels. It is possible, particularly in fossil species, that flaring funnels of epithelial material could have reached well away from the shell edge; similar funnel spines are known in fossil productoids (Muir-Wood and Cooper 1960, pl. 21).

2. Other Bivalvia. Discussions of inhalent and exhalent currents in the Bivalvia usually tacitly assume that the ideal inhalent current is one of constant velocity and magnitude, covering as great a length of commissure as is consistent with other structural demands. There is considerable circumstantial evidence that this view is erroneous. The vast majority of infaunal bivalves receive their inhalent current either down a closely confined siphonal passage or else through a narrow restricted part of the mantle edge. It is likely that gill morphology and function has evolved in step with this, and is in many cases better suited to deal with strong localized inhalent currents than with weak, widely spread ones.

There are other bivalves apart from *Arctostrea* that have conspicuous tubular spines. *Pinna rugosa* Sowerby (Pl. 86, fig. 5) and *Etheria elliptica* Lamarck (Pl. 88, fig. 1) are two of the more striking examples, and it is reasonable to interpret their spines too as reflecting the presence of epithelial funnels that provide the gills with a series of laterally spread, spaced inhalent streams. It is noteworthy that in both these species the spines are only open to the exterior when they are situated right at the very edge of the shell; as soon as they have been displaced even slightly dorsally by further mantle expansion and shell secretion they are sealed off with a thin layer of shell. There is a definite need for observational and experimental evidence to test this theory; but even should it ultimately prove to be untenable it is certainly the most reasonable explanation for these tubular spines in our present state of knowledge. None of the paradigms for other favourite functions attributed to spines (sensory, camouflage, protective, etc.) is closely approached by the morphology of the spines of *rugosa* and *elliptica*. In particular, none of these functions will fit in with the known ecology of *Etheria*—cemented to rocks in the rapids of fast flowing, turbid freshwater rivers. Yet the funnel hypothesis might well be particularly applicable here; for *Etheria* has a conspicuously elongated shell in a dorso/ventral direction. If this should be oriented parallel to the flow of the river, with

EXPLANATION OF PLATE 89

Figs. 1, 2. *Lopha folium* Linnaeus, phenotype *folium*, Recent, Farsan Islands, Red Sea. $\times 1$. External and lateral view of a left valve, attached to a thin twig by the secretion of clasping spines. Note the dorsal diminution of amplitude of the zigzag commissure. SM D.20866.

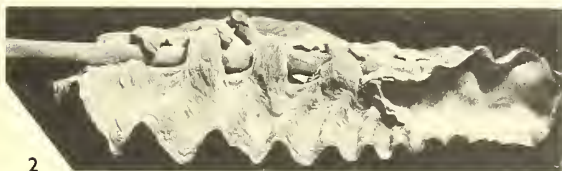
Figs. 3, 4. *Lopha folium* Linnaeus, phenotype *cristagalli*, Recent, unlocated. $\times 1$. External and lateral view of a double valved specimen. Note the large amplitude of the zigzag commissure and the secretion of spines as 'props' for assisting in stability of fixation. UMZC 2002 (Saul Collection).

Figs. 5, 6. *Lopha folium* Linnaeus, phenotype *bresia*, Recent, unlocated. $\times 1$. External and lateral view of a double valved specimen. Attachment is in this case by cementation of a large area of the left valve (reflected in the large unornamented area on the right); the zigzag commissure is of a moderate amplitude. UMZC 2003 (Saul Collection).

Fig. 7. *Pycnodoute hyotis* (Linnaeus), Recent, unlocated. $\times 2$. An extreme example of development of funnel spines at the crests and troughs of a strong marginal zigzag. UMZC 2001 (McAndrew Collection).



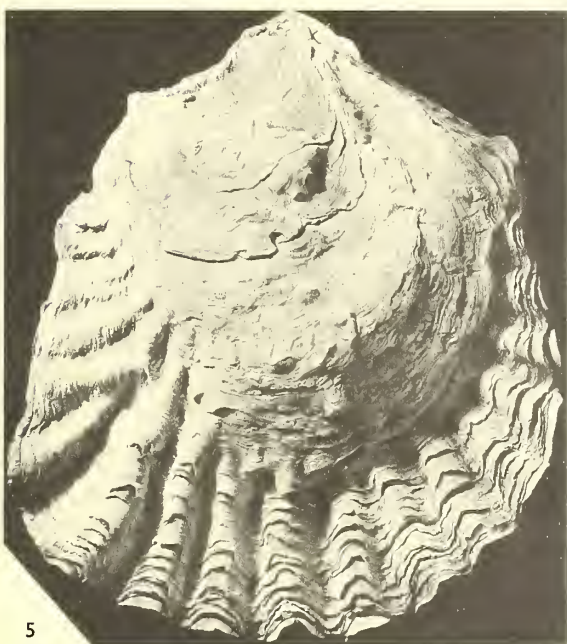
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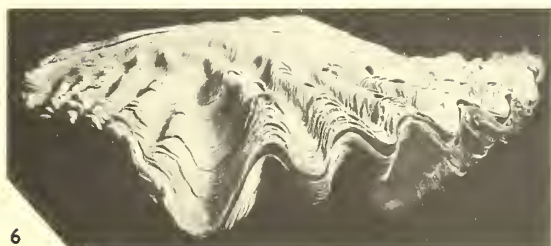
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the dorsal end upstream, then an advantageous eddy effect could well be created around the spines on the ventral periphery.

Many other species of oyster possess funnel spines of greater or lesser significance. *Pycnodonte hyotis* (Linnaeus) is one species that has beautifully moulded funnel spines placed in the crests and troughs of its marginal zigzag (Pl. 89, fig. 7). Even more striking is the juvenile stage of *Crassostrea echinata* (Quoy and Gaimard) (Pl. 88, fig. 2). At a very early stage after spatfall this species has secreted a most complex set of funnel spines. In the light of its favoured habitat of mangrove swamps, it would seem certain that the epithelium lining these spines directly aids the circulation of uncontaminated water and indirectly helps to provide an adequate oxygen supply to the animal. At a slightly later growth stage, the spines become less obviously funnel-shaped, but project as long tubular structures reaching well away from the shell edge. The animal is presumably at this stage even more concerned with gathering an inhalent current stream from as far away from its mangrove attachment site as possible (the roots to which these animals are attached are generally covered with an evil-smelling slime). There are no spines at all in the adult growth stage, perhaps because the left valve of the shell is by then large enough to ensure that the mantle edge is removed from immediate proximity to the substrate.

RECENT OYSTERS: TURBID WATER ADAPTATIONS

Students of Recent oysters currently recognize two major groupings into the genera *Ostrea* and *Crassostrea*. These genera are distinguishable on several counts, but the major structural difference is the presence in *Crassostrea* of an exhalent passage dorsal to the posterior adductor in the right valve; this passage is termed the *promyal chamber*, and ever since its discovery by Nelson (1938) it has been envisaged as an adaptation enabling *Crassostrea* to inhabit turbid waters. This hypothesis agrees well with the known preference of *Ostrea* for offshore clear water, whilst *Crassostrea* favours a muddy estuarine habitat. Such an ecological distribution might also be suggested to be linked to the other major difference between the two genera: *Crassostrea* is oviparous, and *Ostrea* is larviparous.

In a lucid comparison of local American species of *Ostrea* and *Crassostrea*, Menzel (1955) listed several adaptations, additional to the presence of a promyal chamber, that he considered to increase the efficiency of life in turbid waters; most of these adaptations were connected with the development of better cleansing mechanisms.

It is especially noteworthy that *Crassostrea* has more frequent snapping of the valves to eject pseudo-faeces, regardless of the turbidity of the water that it is placed in, and this is linked to a tendency to form and expel much larger quantities of mucus and pseudo-faeces than does *Ostrea*. Two further adaptations come into play in really turbid water: first, the tentacles of the mantle edge are intermeshed, and thus form a partial guard against excessive amounts of sediment entering the mantle cavity; and second, there is the formation of what Nelson (1938) has termed 'pseudo-siphons' in the presence of very heavy suspensions. These pseudo-siphons are formed by contraction of the mantle edges of the right valve to form a groove along which entering particles are then funnelled. In *Crassostrea* there is one inhalent pseudo-siphon, and two exhalent, the second corresponding to the presence of the promyal chamber.

It should further be noted that of all the adaptations serving for greater efficiency in turbid waters, only the promyal chamber involves a structural adaptation; all the other mechanisms, whose efficacy can scarcely be doubted, involve only behavioural adaptation. There is, therefore, no reason to suppose such adaptations to be limited to *Crassostrea*, and, indeed, Menzel makes it clear that Recent *Ostrea* also possesses most of these behavioural adaptations, but to a very much lesser degree than does *Crassostrea*.

Because it involves a structural adaptation, the presence of a promyal chamber can be inferred in fossil species, and, as pointed out earlier, there can be no doubt that *Arctostrea* did not possess a promyal chamber. However, it is virtually certain that the environment favoured by *Arctostrea colubrina ricordeana* was one that could become locally extremely turbid should something disturb the bottom sediment. It would therefore seem inherently highly likely that *ricordeana* (and probably many other species of *Arctostrea*) possessed behavioural adaptations similar to those outlined above for Recent oysters. These would include tentaculate mantle edges, the frequent ejection of pseudo-faeces, and the formation of pseudo-siphons. It is likely that in spite of the large flow of water through the whole shell, brought about by the large gill and branchiform shape, there was a concentrated exhalent flow just posterior to the adductor muscle where the anus debouches its load. The presence of a double plica in the shell edge of occasional specimens of *Arctostrea* (e.g. Pl. 88, fig. 3) at this point is strong evidence for the presence of persistent pseudo-siphons here.

One further facet of the habits of Recent oysters is relevant to discussion of *Arctostrea*. Oysters are in constant danger of being buried under their own pseudo-faeces, together with encroaching sediment. Nelson (1938) observed that 'through . . . movements of the valves, together with adaptive adjustments of the mantle borders, the oyster on soft bottom clears an open zone about itself, and wards off encroaching mud'; and Lund (1957) has shown that even at relatively low turbidities (70–95 per cent. light transmission), oysters on the bottom of an aquarium which has no through currents will completely bury themselves in 36 days.

EXPLANATION OF PLATE 90

- Fig. 1. '*Lopha*' *semitiplana* (J. de C. Sowerby), Upper Chalk, Hartford Bridge, Norwich. $\times 1\frac{1}{2}$. Left valve of a double valved specimen that was attached in life to a straight cylindrical object. Note the few, spaced, strong ribs. SM B.6803.
- Fig. 2. '*Lopha*' *semitiplana* (J. de C. Sowerby), same locality as 1. $\times 1\frac{1}{2}$. Internal view of a right valve displaying well the gill attachment scar ventral to the adductor; note also that the dorsal margin of the adductor scar is convex dorsally. SM B.6796.
- Figs. 3 and 4. *Arctostrea pusilla* (Nilsson), Upper Chalk, Norwich. $\times 1\frac{1}{2}$. Right and left valves of a well-preserved specimen probably attached in life to a belemnite. SM B.1122; figured by Woods, plate 47, fig. 11.
- Fig. 5. *Arctostrea pusilla* (Nilsson), Upper Chalk, Fareham, Hants. $\times 1\frac{1}{2}$. Internal view of a right valve. Note the lack of any gill attachment scar, and the fact that the adductor scar has a dorsal border concave dorsally. SM B.66558.
- Fig. 6. *Arctostrea pusilla* (Nilsson), same specimen as figs. 3, 4. $\times 2\frac{1}{2}$. Lateral view. Note the open crested plicae, and the dorsal diminution of amplitude of the zigzag.
- Figs. 7 and 8. *Arctostrea pusilla* (Nilsson), Cambridge Greensand. $\times 2$. Specimen attached to an ammonite shell, and hence reflecting the shape of an ammonite in its own shell form. BM LL26835.
- Fig. 9. *Arctostrea pusilla* (Nilsson), grey Chalk Marl, Folkestone, Kent. $\times 2\frac{1}{2}$. BM LL26830.
- Fig. 10. *Arctostrea pusilla* (Nilsson), Cambridge Greensand. $\times 2\frac{1}{2}$. Specimen attached to an ammonite shell. BM LL26837.



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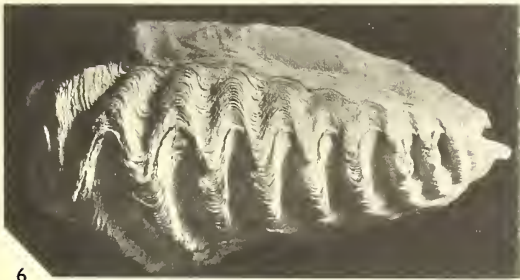
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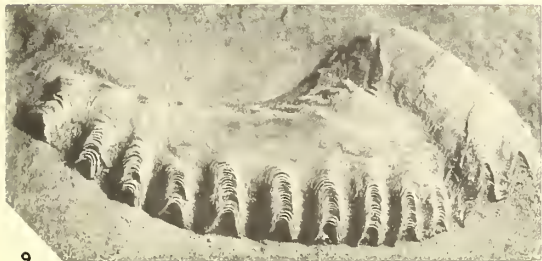
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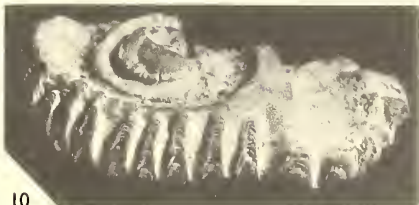
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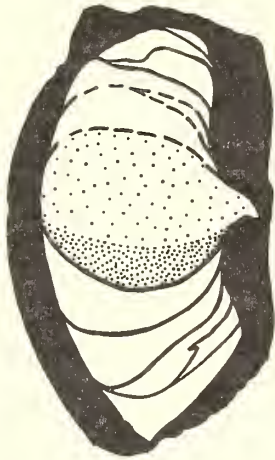
It is obvious that the narrow, high shell of *Arctostrea* is ideally shaped to avoid problems of this sort. Though one would hesitate to assign any primary functional significance to this aspect of over-all shell shape, it must certainly have been a beneficial side-effect of the over-all morphology.

THE ITERATIVE EVOLUTION OF ZIGZAG VALVE EDGES

It is easy to understand how 'pre-adapted' the ostreiform mode of life is for the iterative evolution of zigzag valve structures. As oysters usually settle on flattish surfaces, and as initial shell form is entirely dictated by the shape of the attachment surface, the gills of a juvenile oyster of any kind must of necessity be a thin, high W. But should there be at any subsequent stage a tendency for shell secretion to continue whilst mantle expansion is inhibited, i.e. any tendency for the formation of a vertical zone, then the gill of necessity (because it is attached to the valve interior laterally) becomes phenotypically a broader, less acutely angled W. Now the attachment surface, of course, is rarely quite flat and may in fact be possessed of considerable relief; this relief, again inevitably, is reproduced in the growing edge of the vertical zone, and we thus have a ready-made undulose commissure.

These two phenomena, lateral widening of the gill-W and the inception of an undulose commissure, may both be predicted to occur phenotypically in a proportion of any population of oysters; the first is an inevitable result of building a vertical zone, and the second an additional result of this plus the irregularity of most attachment surfaces. On selection, there will be a tendency for mutations in a similar direction to accrue in the gene pool of a population in which it was advantageous to possess a zigzag valve edge and a widened gill. Thus an initially phenotypic undulose commissure might be rapidly transformed into a genetically stable and functionally more efficient zigzag commissure.

There is obviously a limit to the amount of lateral widening that the gill can accept without detrimental effects on its basic physiology. It would seem that *Arctostrea* has exploited this structural plasticity almost to that limit; internally the genus secretes a series of calcareous plates (or septa, text-fig. 11) which serve to keep the floor of the valve (and therefore the lateral edges of the gills) progressively in line with the crests and troughs of the zigzag (Pl. 85, fig. 2). In other words, the depth of the body cavity is adjusted so as to coincide with the amplitude of the peripheral zigzags, thus ensuring that the most lateral parts of the gills are kept in a zone of continued strong inhalent currents.



TEXT-FIG. 11. *Arctostrea colubrina* (Lamarck), Chalk Marl, near Cambridge. $\times \frac{2}{3}$. A cross-section through the closed shell some distance distal to the adductor; view looking distally. Note the deep body cavity (infilled with sediment, stippled) and the presence of a series of calcareous plates, or 'septa' (all calcareous shell material in solid black), separated by cavities. SM B.6594.

CONCLUSION

The interpretation of the morphology of *Arctostrea* as dominantly due to increased efficiency of feeding and cleansing habits has the major advantage that it enables the morphology to be understood as an integrated whole. The animal can be viewed as 'all adaptation', and not merely as a bundle of discrete adaptations. The shape and detailed morphology of *Arctostrea* are the result of selection for an ever larger and more efficient set of gills. The subsidiary, but important, adaptation found in *A. colubrina ricordeana* was initially a phenotypic response to a specific and difficult environmental regime; though it is not possible to demonstrate rigorously, it would seem likely that the spines characteristic of this subspecies became incorporated in the genotype before its early extinction.

Acknowledgements. I should like to thank Professor H. B. Whittington for making available the facilities of the Sedgwick Museum, Cambridge; and Dr. J. D. Taylor, Dr. N. J. Morris, Mr. A. G. Brighton, and Dr. A. Bidder who kindly gave access to collections in their care. I am indebted to Drs. R. Cowen, K. A. Joysey, and M. J. S. Rudwick for their critical and extremely constructive reading of the manuscript of this paper. The work was carried out during the tenure of a Commonwealth Scholarship, awarded by the British Council.

APPENDIX: TAXONOMIC NOTES ON *ARCTOSTREA*

It is customary in England to use the generic name *Lopha* for oysters throughout the Jurassic and Cretaceous that possess a plicated valve edge of any type. This usage obscures the fact that there are, in fact, several morphologically discrete groups of oysters which happen to possess in common the character of a more or less plicate valve edge. Indeed, if anything is commoner in the Ostreidae than the iterative evolution of gryphaeate shape, it must be the repeated evolution of plicate valve edges.

The type species of *Lopha* Bolten 1798 (and also of *Alectryonia* Fischer 1807) is *Ostrea cristagalli* (Linnaeus), a Recent species from the Indo-Pacific with very coarsely plicated commissure, and a generally rounded valve outline. Thomson (1954) has placed this species in synonymy with *Ostrea folium* Linnaeus, which species is thought to contain three phenotypic variants formerly considered as discrete species—*cristagalli* Linnaeus (Pl. 89, figs. 3, 4), *folium* Linnaeus (Pl. 89, figs. 1, 2), and *bresia* Iredale (Pl. 89, figs. 5, 6). Even allowing for the notoriety that oysters have achieved as variable animals, there is still sufficient morphological range here to tempt even the most conservative to establish two genera for its accommodation. Yet Thomson, after a close study of the animals as well as shells, is quite specific that it 'is inescapable that this is one species which responds variably according to the substrate and to degree of immersion' (p. 148).

Oysters with plicated valve edges are common in the Chalk, and fall into three quite distinct morphological groups. Only one of these groups—that of *Lopha semiplana* (J. de C. Sowerby) (Pl. 90, figs. 1, 2)—is at all reasonably placed in *Lopha* s.s.; the other two groups are best placed in the genus *Arctostrea* Pervinquière 1910. They are *Arctostrea colubrina ricordeana* d'Orbigny and *A. pusilla* (Nilsson).

'*Lopha*' *semiplana* (J. de C. Sowerby)

In his detailed monograph on Cretaceous Bivalvia, Woods (1899–1913) carefully discussed the forms of *Lopha* known in the Upper Chalk horizons and concluded that there was only one valid common species, that of *L. semiplana*. That this species was very variable was both explicitly noted and implied by the vast synonymy that was quoted. Examination of large numbers of Chalk oysters has convinced me that there are two quite distinct forms presently included in *L. semiplana* (Sowerby) *sensu* Woods, and this is confirmed by an examination of type material held in the Norwich Museum and British Museum (Natural History). Whether these two forms represent genetically different species, or whether they are merely phenotypic variants of a single species, is a moot point. In the light of Thomson's

work on the Recent *L. folium* it is virtually impossible to state categorically that any two oysters collected from the same horizon are not conspecific, no matter how different their morphology. However, amongst several hundreds of specimens I have not seen a single one that is not obviously one form or the other, and this points to their being true genetically isolated species; it is, however, conceivable that they represent phenotypes responding to two quite different environmental niches, and that the lack of intermediates is due to the lack of intermediate environmental niches.

The two forms are illustrated on Plates 87 and 90. The true *L. semiplana* has a large irregularly rounded shell (Pl. 90, figs. 1, 2) and is usually attached either to a large flattish surface, or to other specimens of its own kind, or to thin branching objects. It possesses a few (commonly less than 12) broad undulations around the free margins of the commissure which give rise to rounded spaced ribs on the shell surface during shell growth. There is conspicuous crenulation of the margins on either side of the ligamental area, often spreading some distance distally around the commissure; often a well-marked and characteristic gill attachment scar is visible just antero-ventral to the adductor muscle (Pl. 90, fig. 2). The adductor muscle scar itself is large, and has a dorsal margin that is usually *convex* dorsally (Pl. 90, fig. 2); in rare specimens it may be straight.

Of the two specimens originally figured by Sowerby (1812–46, pl. 489) only one, the larger and left hand of the two specimens, is still known. It is here designated lectotype, and is in the collections of the British Museum (Natural History).

The other form has a small lozenge-shaped shell generally reflecting, as Woods pointed out, the preferential attachment to a *Belemnitella*, crinoid stem or similar object. When the attachment surface allows, this species develops the branchiform shape so characteristic of *Arctostrea* (Pl. 90, figs. 3, 4). It possesses a plicated commissure, but the plicae are sharp, numerous (rarely if ever less than 17; commonly over 40), and of the type described as open-textured earlier in this paper (cf. Pl. 86, fig. 6; Pl. 90, figs. 6, 9). The ligament area is small, and without the very marked central pit of *semiplana* s.s., and though crenulations on either side of the ligament area may be developed, they are generally somewhat inconspicuous. The adductor scar is of moderate size and has a dorsal border that is markedly *concave* dorsally (Pl. 90, fig. 5).

The earliest British name available for this form is *Ostrea alaeformis* S. Woodward 1833. Of the three specimens originally figured by Woodward, only one, that of his Plate 90, fig. 3, is still extant. It is here re-figured (Pl. 87, figs. 1–3) and designated lectotype. However, there is an earlier named species of this type from the Upper Cretaceous of Scandinavia—*Ostrea pusilla* Nilsson 1827. Unfortunately the type of *pusilla* is missing from the collection of Nilsson's types at the University Geology Museum, Lund, but there are many specimens of a small *Arctostrea* conspecific with *alaeformis* in Swedish Upper Cretaceous ('mammillatuskrita') faunas. Following Woods's monograph, these specimens are usually labelled as *semiplana* Sowerby, but occasionally an early label reveals that this is the form called *pusilla* Nilsson by Scandinavian workers of the pre-Woods era. On balance, it seems best to adopt the name *pusilla* for this species and to place *alaeformis* in synonymy accordingly.

Though *pusilla* is common in Britain only in the Middle and Upper Chalk, rare specimens from the Cambridge Greensand (Pl. 90, figs. 7, 8, 10) and the Lower Chalk (Pl. 90, fig. 9) demonstrate that it was present in British seas as early as the Cenomanian. These early occurrences are interesting for they serve to show that the species was sympatric with its relative *Arctostrea colubrina*. These early specimens seem to show a strong preference for attachment to ammonite shells (Pl. 90, fig. 10), though this may be due to the small number of specimens available for study.

The introduction of Arctostrea. This name was first introduced as a subgenus of *Alectryonia* by Pervinqui re 1910a. The subgenus—based on *Ostrea carinata* Lamarck from the Cenomanian of Le Mans—received the immediate approval of Douvill .

Alectryonia, as noted earlier, is an absolute synonym of *Lopha*, the two genera being based on the same type species; but, anyway, modern European practice is to use *Lopha* and *Arctostrea* as discrete genera, which course is followed in this paper.

Ostrea carinata Lamarck 1806 (Pl. 86, fig. 2; Pl. 88, figs. 4, 5) possesses well the characters that Pervinqui re and Douvill  used to distinguish the group they called *Arctostrea*. Particularly diagnostic is the branchiform shape, the sharply zigzagged commissure, and the presence of low, rounded, divaricating ribs on the flattened shell top (Pl. 86, fig. 2). Unfortunately, the name *carinata* is pre-occupied by *Ostrea carinata* O. C. Schroeter 1802. However, Pervinqui re (1910b) has already provided

reasons for treating *carinata* Lamarck 1806 and *colubrina* Lamarck 1819 as merely varieties of a single species, and his excellent plates enable one to agree with this conclusion. Thus, though the genus *Arctostrea* must continue to be based on the holotype of *O. carinata* Lamarck, it is permissible to use the name *colubrina* for this group of Cenomanian forms. It may well transpire that a new subspecific name is necessary for the Le Mans *carinata* population, but this must await a thorough revision of the whole genus.

Cox (1962) has adopted the name *colubrina* Lamarck for the English Cenomanian populations of *Arctostrea*. However, there are definite differences between the fossils from Le Mans and the typical English specimens. Conspicuously the English specimens (Pl. 86, fig. 1) have a more open commissural zigzag of greater wavelength, besides possessing the long 'snowshoe' spines described elsewhere in this paper; for their part, the Le Mans specimens have a zigzag of small wavelength, and the presence of conspicuous funnel spines (Pl. 88, fig. 4) results in the strong development of divaricating ribs on the flat top of the valve (Pl. 86, fig. 2). Accepting, on the authority of Coquand (1869), that the name *Ostrea ricordeana* d'Orbigny 1850 refers to a Cenomanian *Arctostrea* possessing long 'snowshoe' spines, it is convenient to distinguish the English forms as *Arctostrea colubrina ricordeana* (d'Orbigny).

It remains to give brief mention to other English members of *Arctostrea*. The common Jurassic species '*Lophia*' *gregarea* (J. de C. Sowerby) is certainly an *Arctostrea*, and ranges from the Bathonian up to the Kimmeridgian. The genus is not found again in any numbers until the Aptian, where it is a common constituent of the faunas of the Lower Greensand on the Isle of Wight, at Farringdon, and Upware. Woods (1899–1913) considered that these forms were conspecific with the chalk populations, but there are significant differences that warrant the resurrection of the name *macroptera* J. de C. Sowerby. The chalk populations themselves are concentrated at two localities—those of Haslingfield and Folkestone. Specimens of *Arctostrea* are known from other scattered quarries in the Lower Chalk (e.g. Norman Cement Works, Cambridge; Cherry Hinton quarry, Cambridge), but are very rare.

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R. M. CARTER
Sedgwick Museum
Cambridge
Present address:
Department of Geology
University of Otago
Dunedin, New Zealand

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SHELL STRUCTURE OF THE BILLINGSSELLACEAN BRACHIOPODS

by ALWYN WILLIAMS

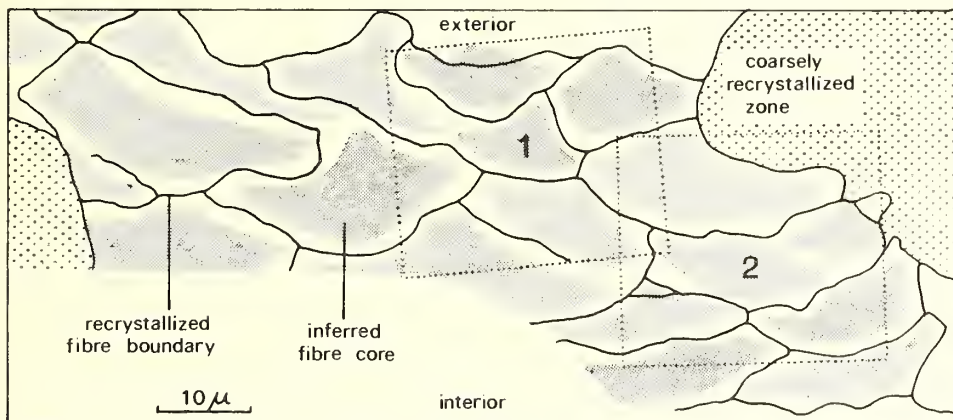
ABSTRACT. Sections of Cambrian articulate brachiopods from the U.S.S.R. show that the calcareous shell of the billingsellacean Nisusiidae probably consisted of normally developed primary and secondary layers with orthodoxly stacked fibres. Disposition of the recrystallized fibres further suggests that whereas *Nisusia* was impunctate, the related *Kotujella* was permeated by simple canals which must have been indistinguishable from the caeca accommodated within endopunctae of younger, unrelated articulate brachiopods.

THIS note is intended as an addendum to the Special Paper on 'Evolution of the shell structure of articulate brachiopods' (Williams 1968) in that it supplements the information contained in that paper on the ultrastructure of the primitive articulate shell. When comparative studies of shell fabric of living and extinct articulate brachiopods were started, it was hoped to conduct a preliminary survey of the subphylum by examining representative genera drawn from all currently recognized superfamilies. This aim was largely achieved although, as stated in the Special Paper (p. 37), the taxa sampled did not include any billingsellaceans or, for that matter, any Lower Cambrian articulates. Such omission was particularly tantalizing because it involved *Nisusia* and related forms which, as the most primitive articulates yet discovered, are morphologically and stratigraphically nearest to the ancestral prototype. Suitable material was not lacking for want of help from many colleagues. Dr. J. Bergström of the Palaeontological Institute, Lund University, Dr. H. Brunton of the British Museum (Natural History), Dr. G. A. Cooper of the U.S. National Museum, and Dr. H. Mutvei of the Riksmuseum, Stockholm had all loaned or given specimens of *Billingsella* (?) *lindströmi* Linnarsson and *Oligomys exporrecta* Linnarsson from the Middle Cambrian of Sweden, and *Eorthis remnicha* Winchell and *Billingsella perfecta* Cooper from the Upper Cambrian of the United States. But when sectioned, the shell fabric of all these specimens was found to have been destroyed by gross recrystallization or by silicification or dolomitization.

It is therefore a matter of great satisfaction to have recently received from Dr. O. N. Andreeva, to whom I am indeed greatly indebted, over 80 specimens of articulate brachiopods from various Cambrian limestone formations of the Siberian Platform, and to find that four of the five genera represented in the collection are well enough preserved to indicate the original style of the shell fabric. Variation in preservation is not obviously related to differences in rock matrix. Specimens of Upper Cambrian *Bajanorthis tukolandica* Andreeva and Lower Cambrian *Nisusia ferganensis* Andreeva contained in grey, coarse, partially dolomitized calcarenites with conspicuous bioclastic constituents up to 1 mm. in size, usually display a discernible fabric, whereas those of *Bobinella kulumbensis* Andreeva which occur with the former species are less well preserved. Moreover, although the shell fabric of the Lower Cambrian *Matutella grata* Andreeva and *Nisusia* cf. *kotujensis* Andreeva, which have been collected from a pale-green marly limestone with more finely divided bioclasts, has been destroyed by recrystallization,

contemporaneous *Kotujella calva* Andreeva, found in the same matrix, is not greatly affected. It thus seems likely that processes of recrystallization or replacement of these shells were as much controlled by local geological conditions as by their texture and the nature of the rock containing them.

Nearly all the shell of *B. tukolandica* and *B. kulumbensis* is made up of recrystallized fibres (Pl. 91, figs. 4–6; Pl. 92, fig. 1) which originally must have been identical in morphology and stacking with those composing the secondary layer of the majority of articulate brachiopods, including the Orthacea and Porambonitacea to which superfamilies the two species respectively belong. Also, where the shell exterior is covered by



TEXT-FIG. 1. Tracing of montage showing the relationship between recrystallized secondary fibres in a transverse section of a pedicle valve of *Nisusia ferganensis* Andreeva, with the inferred outlines of the original fibres; the areas occupied by figs. 1 and 2 of Plate 91 are indicated.

rock, a consistently thin layer of finely crystalline calcite, which is quite distinct from the enclosing granular cement, is seen to form an external skin to the fibres. If this skin represents the primary layer, as seems likely, secretion of *Bajanorthis* and *Bobinella* shells proceeded in the same way as in living rhynchonellides.

Judging from the ultrastructure of the shell, the mantle of *N. ferganensis* is also likely to have functioned in the same way as that of living rhynchonellides. A consistently thin coat of equidimensional grains, sharply distinguishable from the granular cement of the rock, forms an external skin to better-preserved valves and has been taken to represent a recrystallized primary layer. The fibres of the secondary layer, although recrystallized and tending to form aggregates in places, still retain much of the characteristic shape of orthodoxly stacked units (text-fig. 1; Pl. 91, figs. 1–3).

The most unexpected fabric was that found in *K. calva*. Again recrystallization could not disguise the fact that the shell almost certainly consisted of normally secreted primary and secondary layers. Yet the fibres are disposed in arches about $10\ \mu$ wide and $30\ \mu$ apart which are convex outwards (Pl. 92, figs. 2–6). Such deflections could only have been brought about by secretion of fibres around evaginations of the mantle (Williams 1968, p. 30). Their frequency and attitude are strongly reminiscent of the effects of caecal outgrowths from the mantle of endopunctate shells; since they indicate unbranched canals which appear to penetrate both internal and external shell surfaces, they probably accommodated caeca or related structures (text-fig. 2).

In assessing the significance of these Cambrian fabrics to the phylogeny of the articulate shell, some consideration must be given to the affinities of the stocks concerned. The relationships of both *Bajanorthis* and *Bobinella* are incontestible and simply confirm that orthodox primary and secondary shell was as characteristic of the late Cambrian orthaceans and porambonitaceans as of Ordovician representatives of the superfamilies (Williams 1968, pp. 34, 37). It is equally certain that the early Cambrian *Nisusia* with its rudimentary teeth and cardinalia, supra-apical foramen and strong pseudodeltidium is one of the most primitive articulate brachiopods known. These features are also characteristic of three contemporaneous genera, *Eoconcha* Cooper, *Kotujella* Andreeva, and *Matutella* Cooper. On the reasonable assumption that all four stocks are closely related, they have been classified as members of the Nisusiidae which, in turn, has been regarded as the root stock of the Billingsellacea and, more remotely, of all articulate brachiopods (Williams in Williams *et al.* 1965, p. H306). Andreeva (1962, p. 90), however, has drawn attention to the external resemblance between *Matutella* and *Kotujella* and porambonitaceans, and concluded that these two genera should be classified as pentamerides. No one can dispute the superficial likeness between the genera just referred to and certain early Ordovician stocks like *Alimbella* Andreeva. But apart from *Alimbella* having too many orthide characteristics to be generally accepted as a pentameride, there are much more fundamental links between *Matutella*, *Kotujella*, and *Nisusia*, like their possession of supra-apical foramina, poorly developed teeth, and other primitive internal features. In particular, one cannot attach as much importance as did Andreeva (1962, p. 94) to the 'open' delthyrium of *Kotujella* because it was permanently separated from the supra-apical pedicle passage and foramen by a 'concave plate'. It may well be that *Matutella* and *Kotujella* stocks were ultimately ancestral to the porambonitaceans, but that does not diminish the intimacy of their affinities with *Nisusia* and the Lower Cambrian Virginian genus *Eoconcha* (Cooper 1951, p. 5).

In view of the ultrastructure of the shell of *Kotujella* and *Nisusia* it now seems

EXPLANATION OF PLATE 91

Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale, at the bottom left-hand corner of each figure, equivalent to 2 μ .

Figs. 1–3. Transverse and oblique sections of recrystallized fibres of the secondary layer of *Nisusia ferganensis* Andreeva; Lower Cambrian Lensky Beds, Madygen region, Ferganskaya Dolina. Figs. 1 and 2 are part of montage illustrated in text-fig. 1.

Figs. 4, 5. Oblique sections of recrystallized fibres of the secondary layer of *Bajanorthis tukolandica* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia.

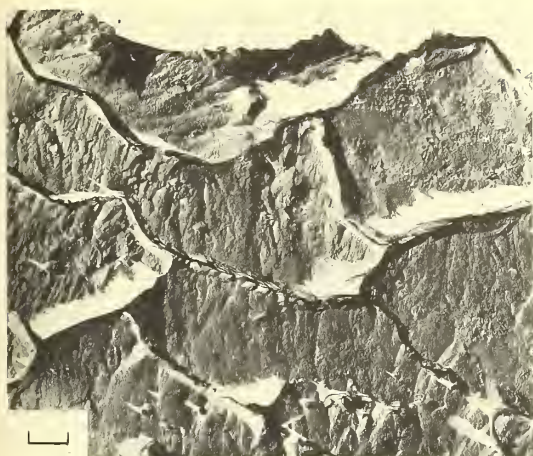
Fig. 6. Oblique sections of recrystallized fibres of the secondary layer of *Bobinella kulumbensis* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia.

EXPLANATION OF PLATE 92

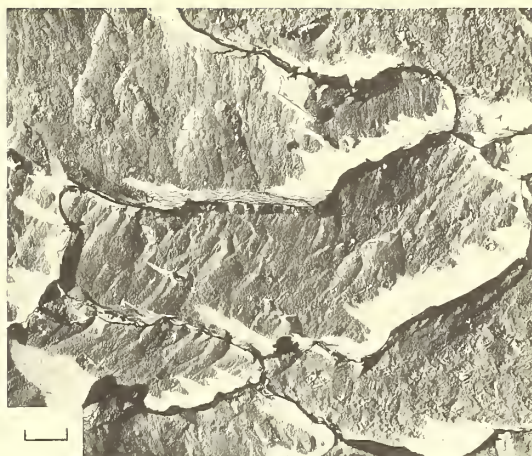
Electron micrographs of single stage negative replicas—cellulose acetate/carbon: shadowed with gold-palladium at 1 in 1. Linear scale at the bottom left-hand corner of each figure, equivalent to 2 μ .

Fig. 1. Oblique section of recrystallized fibres of the secondary layer of *Bobinella kulumbensis* Andreeva; Upper Cambrian limestones, R. Kulyumbe, Vostochnaya, Siberia.

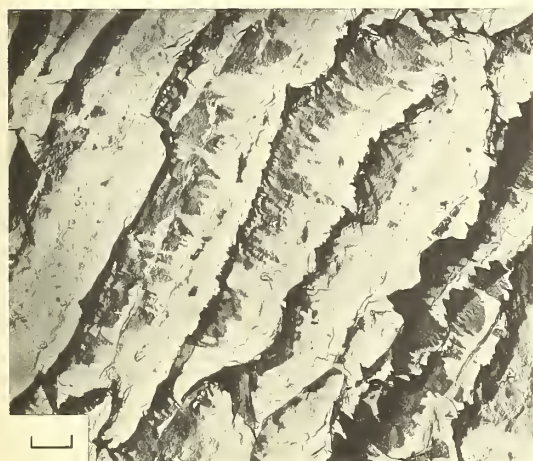
Figs. 2–6. Oblique to transverse sections of recrystallized fibres of the secondary layer of *Kotujella calva* Andreeva; Lower Cambrian Lensky Beds, R. Dakhoi, Vostochnaya, Siberia. Figs. 2 and 4 are part of montage showing vertical range of punctum; figs. 5 and 6 are part of montage illustrated in text-fig. 2.



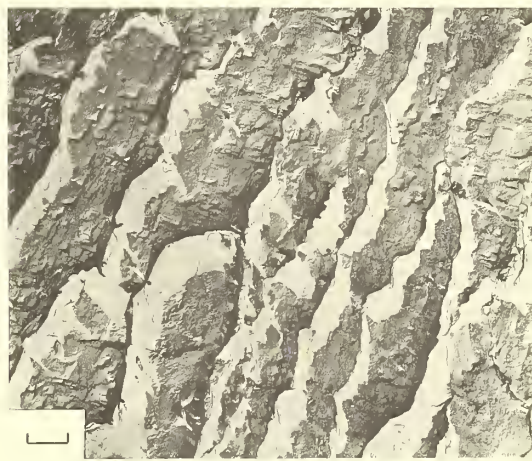
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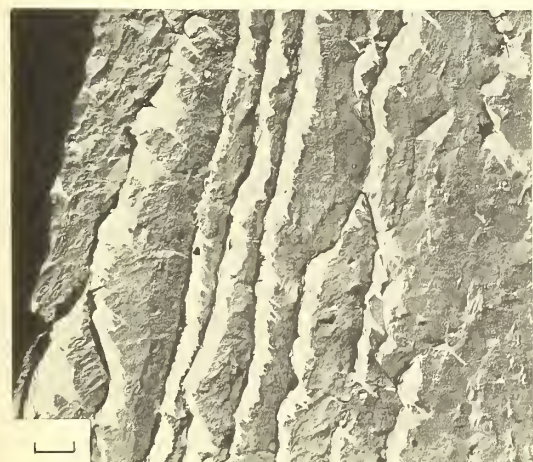
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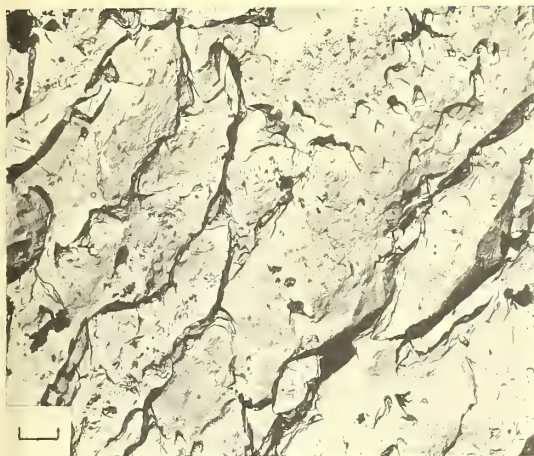
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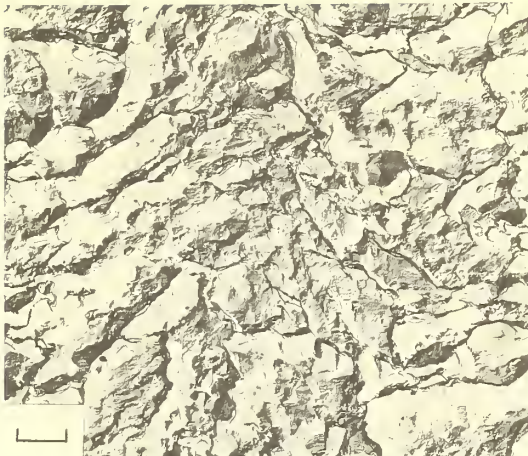
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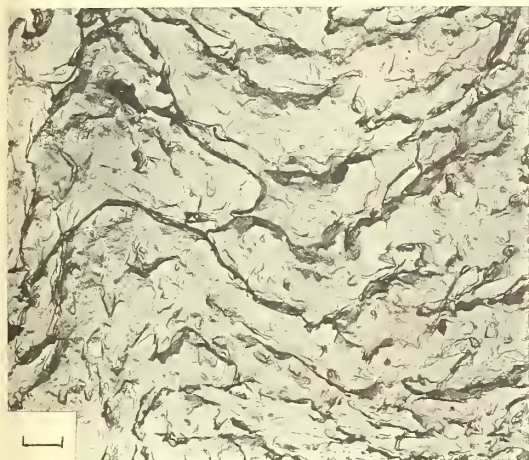
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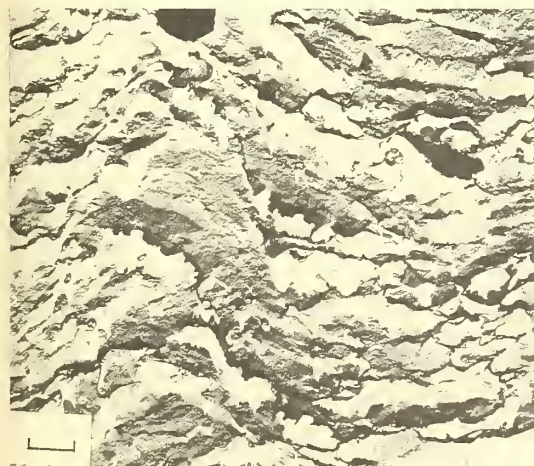
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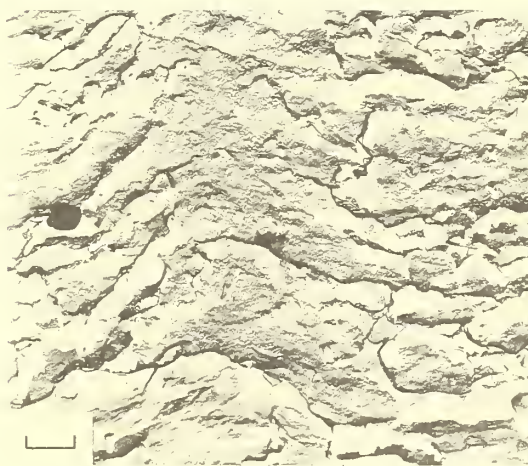
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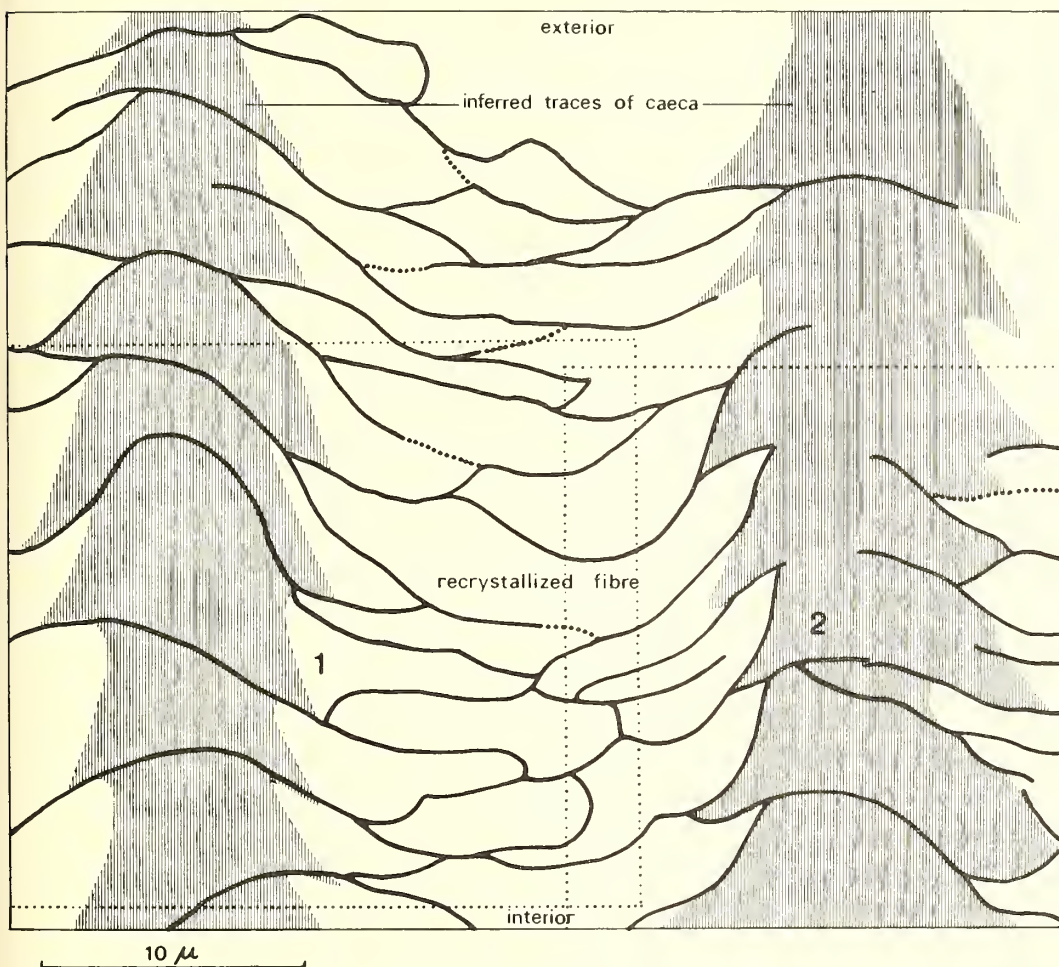


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certain that the nisusiid exoskeleton was secreted as a triple-layered shell composed of an outermost periostracum, a finely crystalline primary layer, and a secondary layer made up of orthodoxy stacked fibres. This being so, the programme of secretion



TEXT-FIG. 2. Tracing of montage showing the disposition of recrystallized secondary fibres in a transverse section of a pedicle valve of *Kotujella calva* Andreeva in relation to two adjacent canals inferred to have accommodated caeca; the areas occupied by figs. 5 and 6 of Plate 92 are indicated as 1 and 2 respectively.

followed by the outer epithelial cells of the mantle of archetypal articulates was the same, even in detail, as that determining the growth of the shell in living rhynchonellides and terebratulides. It is also intriguing to discover that whereas *Nisusia* was impunctate, *Kotujella* bears all the evidence of having been endopunctate, thereby providing yet another example of the independent development of this condition during brachiopod evolution.

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ALWYN WILLIAMS
Department of Geology
The Queen's University
Belfast, N. Ireland

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THREE NEW TETHYAN DASYCLADACEAE (CALCAREOUS ALGAE)

by GRAHAM F. ELLIOTT

ABSTRACT. *Epimastopora malaysiana* sp. nov., from the Malayan Permian, is described from a unique whole solid specimen: normally remains of any *Epimastopora* sp. are extremely fragmentary. Also described are *Harlanjohnsonella annulata* gen. et sp. nov., and *Suppiluliumaella polyreme* gen. et sp. nov., from the Yugoslav and Turkish Cretaceous respectively, and both considered related to *Dissocladella*.

1. EPIMASTOPORA

REMAINS of the genus *Epimastopora* are common at many levels in the Upper Carboniferous and Permian of southern Europe and North Africa, the Middle East, Malaya and Japan, and the south-western United States. They are almost always fragmentary, consisting of small pieces of thin calcareous wall penetrated by numerous close-set canals or pores, and usually seen in thin-sections of limestones. This fragmentation has led to much speculation as to the original form of the thallus (Pia 1923, 1937; Wood 1943; Kochansky and Herak 1960, etc.), and has not been without influence on the synonymy (ref. summary in E. Flügel 1966).

Thin-section remains of whole thalli are extremely rare, though figured by H. Flügel (1963) and Elliott (in press): both of these are of the closely related *Pseudoepimastopora* (Endo 1961).

It is therefore of interest to describe a solid, nearly complete, three-dimensional specimen of *Epimastopora*. This rarity was found in Malayan Permian material collected by Dr. D. J. Gobbett (University of Malaya) and sent by him to me, and I am very much indebted for his permission to describe it.

Family DASYCLADACEAE Kützing 1843 orth. mut Hauck 1884

Tribus CYCLOCINEAE Pia 1920

Genus EPIMASTOPORA Pia 1923

Epimastopora malaysiana sp. nov.

Plate 93, figs. 3, 4

Diagnosis. Elongate cylindrical dasycladacean test with rounded distal termination: calcareous walls very thin and fragile, perforated by very numerous close-set fine cylindrical pores or canals which are themselves subparallel, each with constricted terminal openings to inner and outer wall-surfaces: horizontal (peripheral) rows of pores grouped into fascicules of about seven rows each by sinuous horizontal lines of interruption; these separate but do not space apart the fascicules.

[Palaeontology, Vol. 11, Part 4, 1968, pp. 491-7, pls. 93-5.]

Holotype. The specimen figured in Plate 93, figs. 3, 4 from the Middle Permian, H.S. Lee Mine no. 8, Kampar, Perak, Malaya (Jones, Gobbett, and Kobayashi 1966, p. 324). Brit. Mus. (Nat. Hist.) Dept. Palaeont. V53442.

Other material. One fragmentary specimen, same locality and horizon.

Description. The thallus is hollow-cylindrical in form, with gently curved longitudinal axis, circular cross-section and a rounded sub-paraboloid distal termination; the observed length (incomplete) is 35 mm. and the diameter 7.0–7.5 mm. The thin, very fragile wall is from 0.26–0.31 mm. thick. It is perforated by very numerous close-set fine radial branches or canals, set at right-angles to the longitudinal axis. These canals are straight-sided, the diameter sometimes widening very slightly outwards, but they are rounded at both ends, constricting to open on inner and outer wall-surfaces as circular pores of lesser diameter than the main portion of the intra-mural canal. A thin-section in the very fine-grained powdery dolomite replacing the wall shows the form of the canals, somewhat indistinctly, and suggests that their diameter is probably 0.078 mm. with separating interstices of 0.039 mm.

The wall has broken away distally to reveal the inner core, also of fine dolomite: this shows an outer surface-pattern due to the impression of the inner wall-surface, with detail in reverse. This pattern is of tiny raised circular areas (casts of the inner canal pores), very uniform in size and close-set spacing, about 220 to a complete horizontal peripheral ring. Longitudinally (vertically) the horizontal rows are separated into fascicules of six or seven by sinuous horizontal peripheral lines. These have a characteristic irregular appearance due to the sinuities being independent as between consecutive lines. The distance apart of any two successive lines varies from 0.68–0.78 mm., and this distance, accommodating six or seven rows of pores, is compatible with the inner canal and interstice dimensions inferred from the thin-section.

The outer wall-surface shows a comparable pattern, but the canal terminations show as minute pore-openings in gentle depressions separated by interpore convexities. On rubbed or worn portions the pores are much larger, since the abraded surface intercepts the inner, larger canal-diameters. For this reason, although the pores of the outer surface correspond each to a pore-cast of the inner core-surface, the outer surface has a much less uniform appearance. The sinuous horizontal lines occur, but are much fainter and less obvious. Where a broken edge of the calcareous wall terminates across a sinuous line on the core, the sinuous line of the outer surface, when visible, may be seen to correspond with that on the core.

Remarks. This unique specimen shows that in the living *Epimastopora* calcification was confined to a very thin peripheral zone. The thick core may have been a large non-calcified juicy stem-cell, with presumed endospore reproduction, in which case the

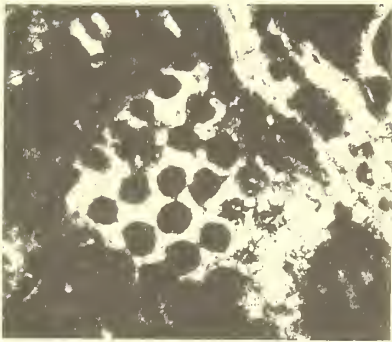
EXPLANATION OF PLATE 93

Figs. 1, 2. *Harlanjohnsonella annulata* gen. et sp. nov. Upper Cretaceous; Fetrebovo, Zlatibor, Serbia, Yugoslavia. 1. Near-transverse thin-section; 2. Tangential thin-section. Both $\times 30$; syntypes. B.M. (N.H.), V53441.

Figs. 3, 4. *Epimastopora malaysiana* sp. nov. Middle Permian; H.S. Lee Mine no. 8, Kampar, Perak, Malaya. 3. Holotype, complete specimen, $\times 3$. 4. Distal portion, enlarged to show detail, $\times 10$. B.M. (N.H.), V53442.



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existing wall-canals described above were minute crowded branches, and their sinuous-fasciculate arrangement may have been a transitional stage from aspondyl to euspondyl branch-arrangement. Alternatively, a thinner non-calcified stem-cell of unknown diameter, could have given rise to euspondyl whorls of non-calcified primaries, in which case the preserved wall-canals are to be interpreted as crowded secondaries or tertiaries in sinuous zones corresponding each to an inner whorl. The fascicules as now seen are to be interpreted not as six or seven adpressed horizontal rows, but as irregular horizontal zones six or seven branches wide. This interpretation is compatible with either of the two reconstructions suggested above.

Although traces of matrix were feebly effervescent with weak acid, both core and wall were completely replaced by fine-grained, friable dolomite. This was difficult to section, and the details of the wall were not distinct, although as stated, the inferred dimensions are compatible with external evidence. Since all other *Epimastopora* spp. are based on clearly sectioned wall-fragments with measurable canals and little else (see tables in Johnson 1963), the present specimen shows so much more that it is described as a new species.

This new evidence on the external form of *Epimastopora* invites comparison with *Koninckopora*, of somewhat similar morphology and also of Upper Palaeozoic age. This latter genus was described in detail by Wood (1943) from solid specimens and many thin-sections.

Both genera show a thin marginal calcification only, giving a thin sheath-like calcified thallus. In *Koninckopora* the infilled cavities representing the branch-terminations are proportionally large, very thin-walled, and adpressed to give a polygonal structure in cross-section. This appearance had led to its earlier interpretation as a coral and as a bryozoan, and only later was it recognized as algal (Wood 1943). In *Epimastopora* the corresponding structures, 'pores', are separate filled cavities within the calcified wall, and although often close-set, are proportionally better spaced and not adpressed. In *Koninckopora* the cells show evidence of sporangial structures in their outer parts, interpreted by Wood from the differential calcification of the infilling. This phenomenon has never been seen by me in very many thin-sections of *Epimastopora*, nor in the related *Pseudoepimastopora*, although in this latter genus the pores have been suggested as sporangial from the swollen morphology.

Wood (op. cit., p. 209) suggested the close relationship and possible identity of *Koninckopora* and *Epimastopora*. In view of the very limited palaeontological evidence from the surviving calcified structures, I regard the two as valid separate genera, both referable to Pia's 'tribe' (or subfamily) Cyclocrineae.

2. HARLANJOHNSONELLA

In material examined by me for Dr. J.-P. Rampnoux (Université d'Orléans-Tours), certain thin-sections showed a profusion of dasyclad debris and fragments: most of this proves to be referable to a new genus. This sample is from transgressive basal Upper Cretaceous, possibly Cenomanian, in the Zlatibor area of SW. Serbia; associated microfossils are fragments of a small *Clypeina* sp. (Dasycladaceae), gastropod and other molluscan shell-debris, and rare crustacean fragments. I am much obliged to Dr. Rampnoux for his kind permission to study and describe the alga.

Tribus THYRSOPORELLEAE Pia 1927 emend. Pia 1936

Genus HARLANJOHNSONELLA gen. nov.

Diagnosis. Weakly calcified thin-walled tubular and annular dasyclad, with successive verticils showing numerous swollen primaries, the presumed secondaries not being calcified. Upper Cretaceous; type-species *H. annulata* sp. nov.

Harlanjohnsonella annulata sp. nov.

Plate 93, figs. 1, 2; Plate 94

Description. Thin-walled, weakly and irregularly calcified dasyclad, length (incomplete) up to 6 mm. seen, external diameter up to and commonly 2.0 mm., exceptionally 2.25 mm., full wall-thickness 0.26 mm., giving a d/D ratio of about 74%, but commonly the calcification is incomplete and hence the stem-cell cavity appears even wider. The dasyclad is annular in structure; these annuli or rings, about 0.19–0.25 mm. thick, readily came apart, and by reason both of their proportions and their weak calcification they fragmented easily, so that the species is largely represented by debris. Each complete annulus shows about 48–50 primary branch-cavities, somewhat crowded so that neighbouring branches are sometimes directed at slight angles greater or lesser than normal from the stem-cell axis. Because of this the alternation in position of branches in successive verticils may appear irregular in tangential section. The branches are pyriform or flask-shaped, communicating with the stem-cell by a narrow pore-neck of 0.013 mm. diameter, and widening rapidly within the wall-thickness to a globular or ovoid cavity of 0.13–0.14 mm. diameter. These cavities are usually open to the exterior by reason of the ragged incomplete calcification of the outer annulus-surface, though exceptional preservation seems to suggest that the swollen cavities divided externally into thinner secondaries.

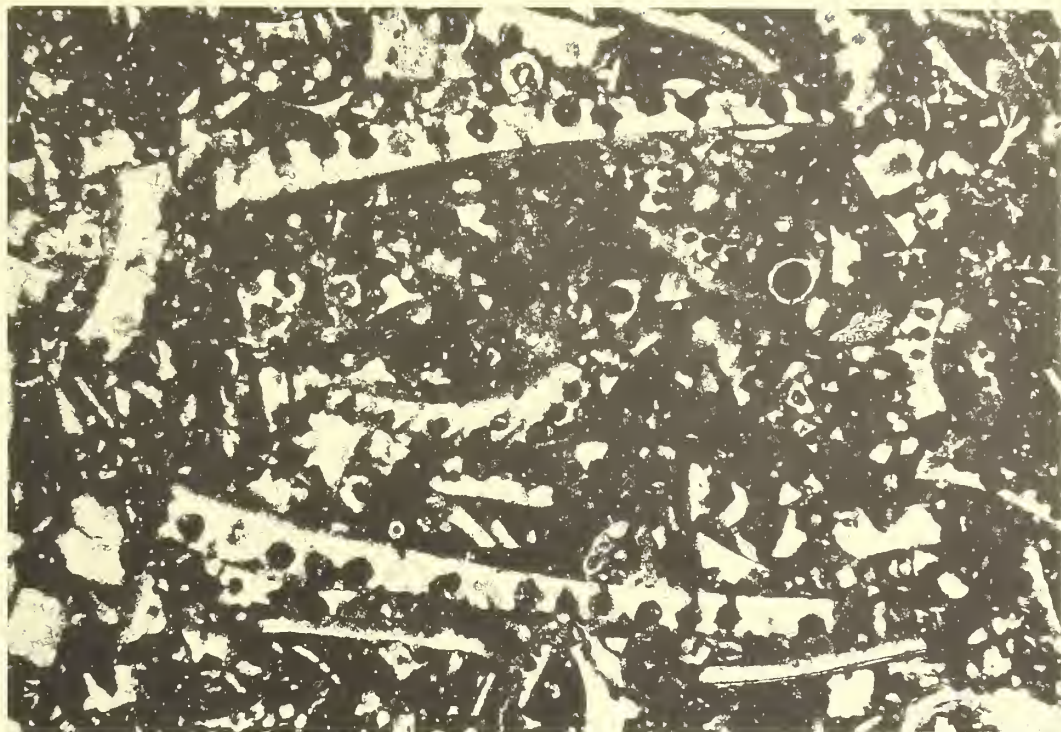
Syntypes. The specimens figured in Plate 93, figs. 1, 2, Plate 94, fig. 1 from the transgressive basal Upper Cretaceous, possibly Cenomanian, of Fetrebovo, Dlaglica, SE. of the Zlatibor massif, SW. Serbia, Yugoslavia. Brit. Mus. (Nat. Hist.) Dept. Palaeont. V53441, 53443.

Other material. Five thin-sections, rock from same horizon and locality.

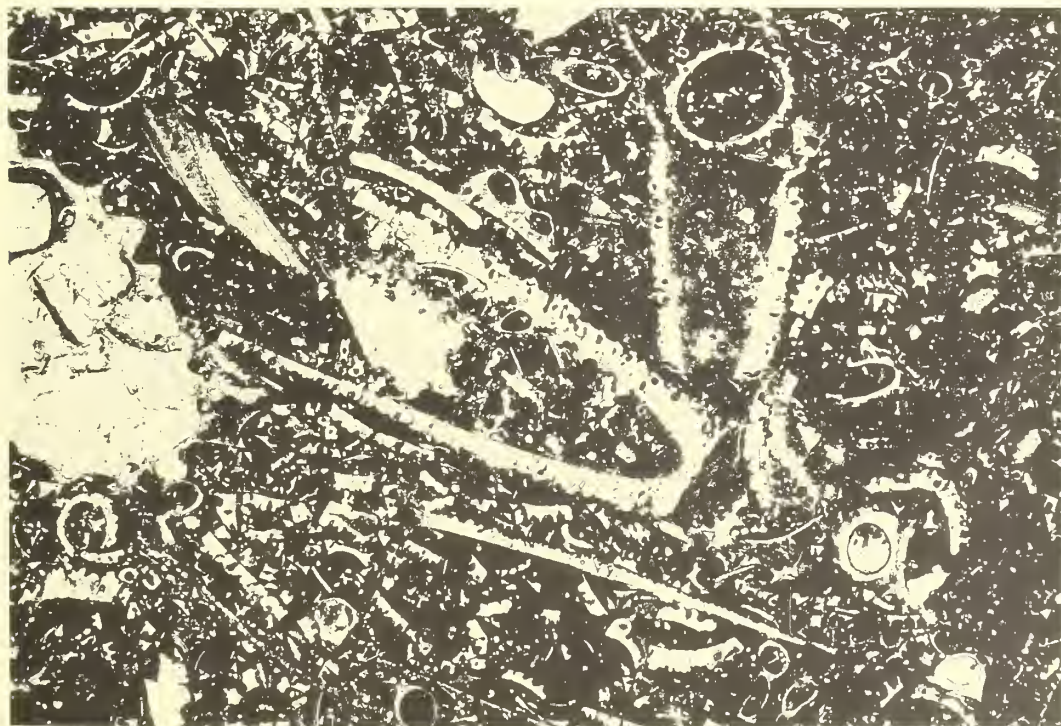
Remarks. *Harlanjohnsonella*, thin-walled, the annuli crowded with simple swollen branches, and fragmentary, brings to mind especially the Carboniferous *Coelosporella*, the Permian *Epimastopora* and *Pseudoepimastopora*, and certain forms referred to the Cretaceous *Neomeris cretacea* Steinmann. From the former three genera it differs in its markedly annular character, the Palaeozoic fragments being random pieces of the thin tubular or flask-shaped thalli. From such forms as the annular *Neomeris cretacea* Delmas and Deloffre non Steinmann, from the Cretaceous (Delmas and Deloffre 1962),

EXPLANATION OF PLATE 94

Figs. 1, 2. *Harlanjohnsonella annulata* gen. et sp. nov. Upper Cretaceous; Fetrebovo, Zlatibor, Serbia, Yugoslavia. 1. Syntype, Longitudinal thin-section, $\times 30$. B.M. (N.H.), V53443. 2. Thin section of matrix with numerous broken and fragmentary *Harlanjohnsonella*, $\times 10$. B.M. (N.H.), V53444.



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it differs in the apparently more simple branch-structure, *Neomeris* spp. showing globular sporangia flanked by thinner sterile branches. A closer comparison can be made with *Dissocladella*, especially the Palaeocene *D. savitriae* (Pia 1936). This species shows annuli of similar size and proportions, each with a similar number of branches, but more strongly calcified. Within this calcification each branch is seen to communicate with the stem-cell cavity by a narrow pore and to swell distally to a spherical body: from this a bunch of four to six thin short secondaries communicates with the outer surface. *Dissocladella* is now known to be represented by species from older Mesozoic to Palaeocene (Ott 1965); it seems likely that the form now described was, in fact, a dasyclad of very similar plant morphology to *D. savitriae* but more weakly calcified, so that no certain evidence of the original secondary branches remains. Geological age and the observed nature of the calcification alike fit with this interpretation. Since there is no direct fossil evidence of the secondary branch-structure the species cannot correctly be referred to *Dissocladella*, all of whose species show calcified remains of the secondary branching. I have pleasure therefore in referring it to *Harlanjohnsonella* gen. nov., in tribute to the distinguished American palaeophycologist Professor J. Harlan Johnson.

3. SUPPILULIUMAELLA

This new and striking Lower Cretaceous genus occurred in Turkish material reported on by me for Professor Fuat Baykal of Ankara University, and I am much indebted to him for permission to describe it.

Genus SUPPILULIUMAELLA gen. nov.

Diagnosis. Strongly calcified thick-walled tubular dasyclad, showing verticils of long thin primaries with large conspicuous terminal swellings, each dividing into very short swollen secondaries. Lower Cretaceous: type-species *S. polyreme* sp. nov.

Suppiluliumaella polyreme sp. nov.

Plate 95, figs. 1-4

Description. Strongly calcified tubular dasyclad; length 6 mm. (incomplete), external diameter 1.82 mm., internal diameter 0.62 mm., with consequent d/D ratio of 34%. Numerous close-set verticils of branches, about five or six verticils per millimetre of tube-length. The calcification extends inwards adjacent to each primary, so that the stem-cell cavity in vertical section has a regularly notched outline, showing as annular bars in vertical section tangential to the stem-cell cavity wall. The primaries joined the stem-cell on the undersides of these annular bars.

Each verticil is estimated to contain about twenty-four primary branches. These branches are initially almost straight, about 0.065-0.078 mm. thick, circular in cross-section and set at an angle of 65-70° from the horizontal, with consequent long oblique courses in the wall thickness. At about the outer third of wall-thickness they turn to an angle of 45° from the horizontal, and form conspicuous swellings, of up to 0.18 mm. diameter. In vertical section the swellings are rounded triangular or shield-shaped, with

apices inwards: in transverse section they are rounded squares or pentagons. Finally, each divides into four or five short closely adjacent rounded-cylindrical secondaries of 0.065–0.078 mm. diameter, which extend to the outer surface.

Holotype. The specimen figured in Plate 95, fig. 1, from the Lower Cretaceous limestones exposed about 16 km. SSE. of Amasya, a Turkish town about 260 km. ENE. of Ankara. Brit. Mus. (Nat. Hist.), Dept. Palaeont. V53445.

Paratypes. The specimens figured in Plate 95, figs. 2–4, from the same thin-section as the holotype.

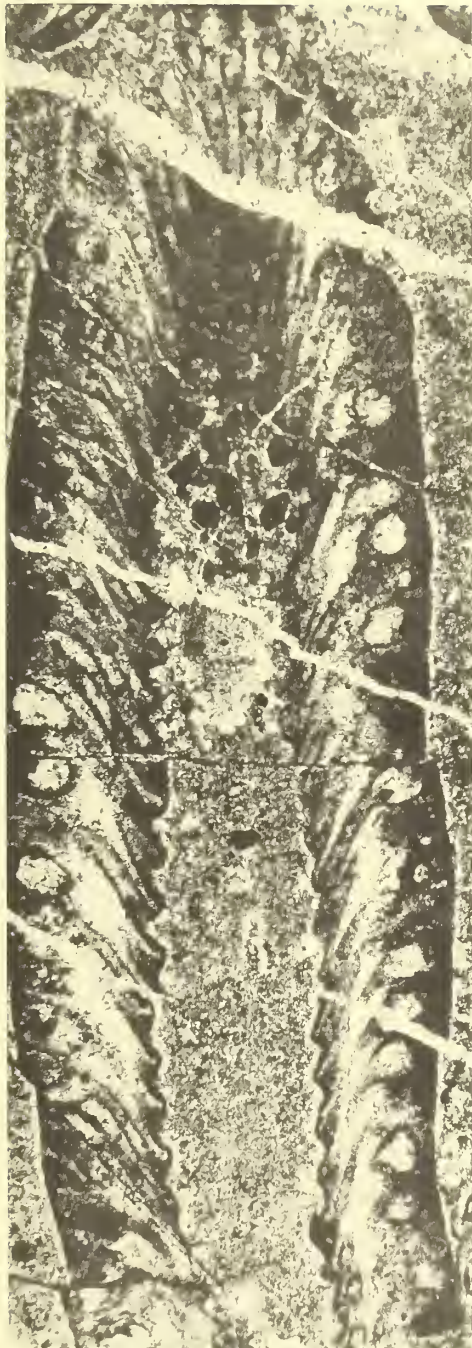
Remarks. This peculiar and distinctive dasyclad shows the basic branch-pattern or plan of a thyrso-porellid, and since it divides after the primary swelling into secondaries only, is closest to *Dissocladella*. However, the proportions of primary, swelling and secondary, and the steep angle at which they occur is quite different to that in any known species of *Dissocladella*, which have very short horizontally set branches. For this reason the Turkish species is made the type of a new genus. The generic name commemorates King Suppiluliuma of the ancient Hittites, whose territory lay in what is now Turkey, and the specific name refers to the numerous oar-like branches as seen in thin-section.

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EXPLANATION OF PLATE 95

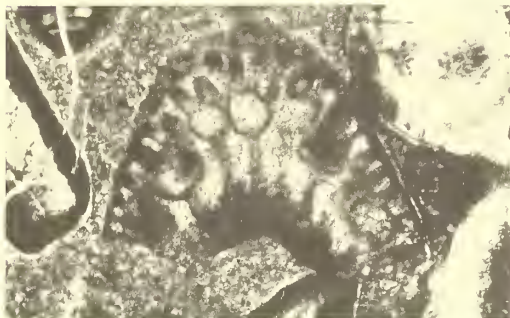
Figs. 1–4. *Suppiluliumaella polyreme* gen. et sp. nov. Lower Cretaceous; 16 km. SSE. of Amasya, Turkey. Thin-sections, $\times 30$. 1. Holotype: longitudinal section. 2. Paratype: outer tangential section to show swellings and secondary branchlets. 3. Paratype: oblique-transverse cut to show form of branches. 4. Paratype: inner tangential section to show annular structures around stem-cell cavity. B.M. (N.H.), V53445.



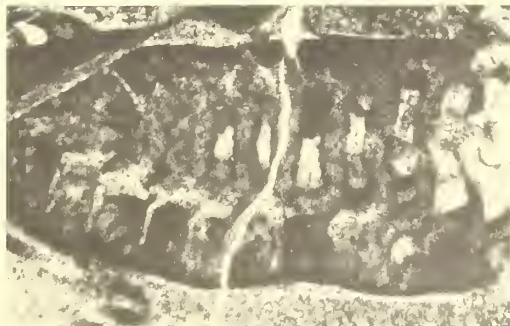
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G. F. ELLIOTT
60, Fitzjohn Avenue
Barnet
Herts.

Typescript received from author 14 December 1967

COLOUR MARKINGS IN *PHACOPS* AND *GREENOPS* FROM THE DEVONIAN OF NEW YORK

by GEORGE C. ESKER, III

ABSTRACT. The colour markings in *Phacops rana* and *Greenops boothi* are described and discussed. It is suggested that *P. rana* had the ability to change its pigmentation. Only four examples of colour markings in trilobites have been mentioned in the literature.

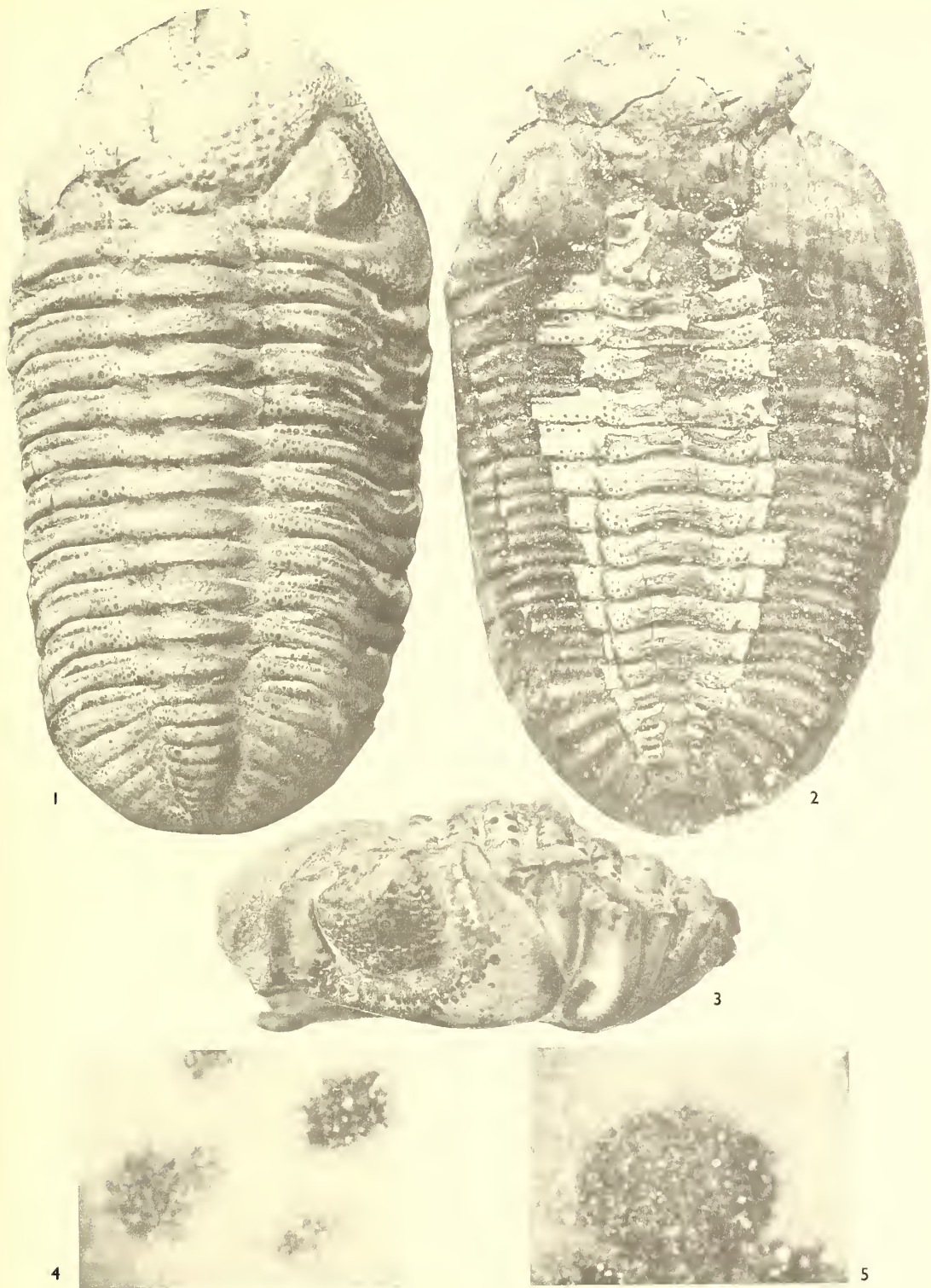
THREE specimens of more or less complete dorsal exoskeletons of trilobites with colour markings have been discovered in the Middle Devonian Hamilton shale at a locality near Alden, New York. Two of these specimens are identified as *Phacops rana* Green 1832, and the third as *Greenops boothi* (Green 1837). The specimens exhibit colour markings in the form of black spots wherever the dorsal exoskeleton is intact and unweathered. The black spots are presumed to be original rather than diagenetic because of their linear arrangement on the pleura and not on the axis and glabella of the specimen of *G. boothi*. The irregularly circular black spots vary in size, are randomly arranged in *P. rana*, and have a linear arrangement in part in *G. boothi*. The black spots are probably melanophores.

The two specimens of *P. rana* have the black spots scattered over the entire exoskeleton. This general pattern appears to be the same as that described by Teichert (1944) as occurring in a pygidium of *Ditomopyge meridionalis* from the Permian of Australia. One of the two specimens of *P. rana* has spots noticeably smaller in size than in the other specimen. Many of the spots are very irregular and show black branches extending out from them. The specimen with larger spots has very short black branches extending outwards. It is assumed that these two specimens belonged to the same species possessing the ability to change its pigmentation, rather than that they show different degrees of fixed pigmentation. This suggests that the specimen with the smaller spots had the pigment contracted into the central area and the main branches. This would make the whole surface of this trilobite lighter to match its background. The specimen with the larger spots has the pigment expanded to occupy nearly all the branches of the melanophores; this individual would therefore be darker to match a darker background. Such an ability to change colour to match its background would

EXPLANATION OF PLATE 96

Figs. 1, 3-5. *Phacops rana* Green. 1, Dorsal view of complete specimen, $\times 3$, Louisiana State University Geology Museum, Type Collection No. 8269. 3, Lateral view of enrolled specimen, $\times 4$, Louisiana State University Geology Museum, Type Collection No. 8271. 4, Portion of left thoracic pleura, $\times 165$, same specimen as 1, contracted pigment. 5, Portion of left pygidial pleura, $\times 165$, same specimen as 3, expanded pigment.

Fig. 2. *Greenops boothi* (Green). Dorsal view of complete specimen, $\times 4.5$. Louisiana State University Geology Museum, Type Collection No. 8270.



ESKER, Colour markings in trilobites

clearly be an advantage to any trilobite. Trilobites having this ability were most probably active, vagrant benthonic forms and not burrowers.

The specimen of *G. boothi* has the colour markings preserved on most of the axis, on a portion of the glabella, and on part of the pleura. On the glabella and axis, the spots are small and entirely random in arrangement. On the pleura, the spots have a secondarily symmetrical arrangement due to the two, generally linear, transverse rows per segment, though the number and the position of the spots varies.

It is probably safe to assume that *D. meridionalis* had the same ability as *P. rana* to change its colour to match its background. Perhaps the eyes would be sensitive to colour changes in the background and served to inform the trilobite of such changes. It is unlikely that trilobites which were either blind or which had reduced vision had this type of camouflage ability. Whether or not *G. boothi* and *Phillipsia? tenuituberculata* as described by Williams (1930) had this same ability, remains open to speculation. Both of these species show at least a partial arrangement of the black spots in rows.

The other two recorded examples of colour markings in trilobites appear to be of an entirely different type. Raymond (1922) described a pygidium of *Anomocare vittata* from the Cambrian of Alabama with slightly irregular light and dark bands becoming narrower across the axis. Wells (1942) reported several examples of *Isotelus maximus* from the Ordovician of Ohio, showing deeper shades of the same colour on different areas of the dorsal exoskeleton. These two types of colour markings are most probably due to carotenoid pigments, different from the melanin pigment forming the black spots occurring in the other cases of colour markings. The banding may have served to conceal the trilobite if it could be matched against an appropriate background.

In conclusion, it seems probable that there were many different types of colour markings in such a diversified group as the trilobites, as there are in modern Crustacea. Of special interest is the apparent ability of individuals of *Phacops rana* to conceal themselves by expanding or contracting the pigment in their chromatophores to match a light or a dark background.

Acknowledgements. The author wishes to thank Dr. W. T. Dean of the British Museum (Natural History) for his criticisms of this paper; also Mr. D. Nugent and Mr. L. Nichols for photographic work.

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GEORGE C. ESKER, III
 Geology Department

Louisiana State University
 Baton Rouge, La. 70803, U.S.A.

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STUDIES ON TRIASSIC FOSSIL PLANTS FROM ARGENTINA. IV.

THE LEAF GENUS *DICROIDIUM* AND ITS POSSIBLE RELATION TO *RHEXOXYLON* STEMS

by SERGIO ARCHANGELSKY

ABSTRACT. The cuticle of four species of the genus *Dicroidium* is described. The material has been found in close association with *Rhexoxylon* stems in the locality of Ischigualasto, San Juan Province, Argentina. Two new combinations are proposed: *Dicroidium zuberi* (Szajnocha) and *Dicroidium elongatum* (Carruthers). It is proposed that *Dicroidium* leaves are related to *Rhexoxylon* stems (a) because they are associated in four Triassic localities of South Africa and Argentina, and (b) because there is a structural relation of both organs with the Palaeozoic pteridosperms.

THIS paper reports the very striking association of *Rhexoxylon* petrifications with *Dicroidium* compressions and impressions in two localities in Argentina, and (though with less clear information) in South Africa.

The Ischigualasto Formation (of NW. Argentina) has yielded abundant petrifications of *Rhexoxylon* stems (Archangelsky and Brett 1961, Brett 1968). The stems can be about 10 m. high and about 1 m. in diameter near the base. Most of the petrifications observed in the field belong to this genus. In the same beds, pockets of loose sandstone with many leaves were also found. Some of these pockets include stems covered by compact masses of cuticles, and the stems are sometimes further surrounded by a thick layer of gypsum in which similar cuticles are embedded. The leaves are fragments consisting of cuticles with only a little internal substance. Four lots of material collected at different times, have been studied. The Archangelsky and Brett collection (1961) and the Romer collection (1964-5) belong to the La Plata Museum Palaeobotanical Collection (LP-PB), while the Archangelsky (1958) and Herbst (1960) material, belongs to the Lillo Institute Collection of Tucumán University (LIL-PB). In the same formation, and in the same area, a very rich vertebrate fauna has been found. Some of the skeletons are also covered by compact masses of cutinized leaves (Romer 1962).

Four species of leaves were found in Ischigualasto, associated with *Rhexoxylon*, and I refer them, on the ground of size and shape of pinnae, and cuticular structure, to the following species of *Dicroidium*:

Dicroidium zuberi (Szajnocha) comb. nov.

Dicroidium elongatum (Carruthers) comb. nov.

Dicroidium coriaceum (Johnson) Townrow

Dicroidium sp.

Only the first three species may be considered as abundant; the fourth is rare and difficult to determine precisely.

The second Argentine locality which has yielded *Rhexoxylon* petrifications and [Palaeontology, Vol. 11, Part 4, 1968, pp. 500-12, pls. 97-8].

Dicroidium impressions is Barreal, San Juan Province. This association is here reported for the first time; the petrifications are now being studied by Dr. Bonetti (Buenos Aires Natural History Museum) who has already published the study of the leaf impressions (1963).

From the literature (Du Toit 1954, Walton 1956) it seems that the *Rhexoxylon-Dicroidium* association is also present in the Triassic of South Africa.

On independent grounds, both *Rhexoxylon* and *Dicroidium* (together with their known male and female fructifications, *Pteruchus* and *Umkonasia* respectively) may be derived from Palaeozoic pteridosperms.

DESCRIPTION OF THE MATERIAL

Genus DICROIDIUM Gothan 1912 emend. Townrow 1957

- 1943 *Dicroidiopsis* Frenguelli
- 1943 *Diplasiophyllum* Frenguelli
- 1943 *Zuberia* Frenguelli
- 1943 *Xylopteris* Frenguelli
- 1957 *Hoegia* Townrow

Discussion. Townrow (1957) emended the original diagnosis of *Dicroidium* (Gothan 1912), making a clear definition of its morphological and anatomical characters. I accept here this definition with the exception of two characters: (a) the cuticle may be thicker than $3\ \mu$ and (b) the stomata may be imperfectly dicyclic as well as dicyclic. In the emended diagnosis of *Dicroidium*, there is no statement of the shape of the pinnules. As *Xylopteris* is here included in *Dicroidium*, pinnules of the genus may be rhomboidal, elongated or linear, with one or several veins in them.

The thickness of a cuticle is of no generic value; it may even vary in one species. Also, the stomata may be variable (from mono- to di-cyclic) in one species of a genus; when the cycles of subsidiary cells are constant, the character may be regarded as specific rather than generic. Accepting these two emendations, the genus *Hoegia* (Townrow 1957) is a synonym of *Dicroidium*. (The forking of the main rachis of the frond was not observed by Townrow in his *Hoegia* specimens, probably because he dealt with small fragments of pinnae. Large fronds of *Dicroidium* are commonly found broken and it is not easy to find the main rachis with its fork.)

Frenguelli (1943, 1944) defined the genus *Zuberia* on external morphology of pinnae; there are no obvious reasons, however, to differentiate this genus from *Dicroidium*, as the shape of pinnules and venation are identical. Townrow (1957) believes that *Zuberia feistmanteli* sensu Frenguelli is in fact *Dicroidium*. Bonetti (1966) goes further and places all four species of Frenguelli's *Zuberia* in *Dicroidium feistmanteli*, but I unite them as a separate species, *Dicroidium zuberi*.

The genera *Dicroidiopsis* (Frenguelli 1943) and *Diplasiophyllum* (Frenguelli 1943) are also placed in *Dicroidium* by Townrow and by Bonetti; I agree with these authors.

Xylopteris (Frenguelli 1943) is here considered as belonging also to *Dicroidium*. Although not expressed in synonymy both Townrow (1962a) and Bonetti (1966) have already recorded this opinion. The cuticular structure of *X. elongata* for instance, in particular the stomatal apparatus, is similar to the cuticular structure of *Dicroidium*

coriaceum (formerly known as *Johnstonia coriacea*). The forking of the main rachis in *Xylopteris* agrees with all known species of *Dicroidium*. The shape of the pinnules, which are linear, is here considered as a character of specific rank.

Dicroidium zuberi (Szajnocha) comb. nov.

Plate 98, figs. 1, 2; text-figs. 1a, 2d, e

- 1888 *Cardiopteris zuberi* Szajnocha, p. 233, pl. 2, fig. 1.
- 1943 *Zuberia zuberi* (Szajnocha) Frenguelli, p. 300.
- 1944 *Zuberia zuberi* (Szajnocha) Frenguelli; Frenguelli, p. 9, pl. iv-xi, pl. xii, figs. 1, 2.
- 1944 *Zuberia feistmanteli* (Johnston) Frenguelli; Frenguelli, p. 3, pl. i-iii.
- 1944 *Zuberia barrealensis* Frenguelli, p. 20, pl. ix, figs. 1, 3; pl. xiii.
- 1944 *Zuberia sahnii* Frenguelli, p. 23, pl. xii, fig. 3.
- 1957 *Hoegia papillata* Townrow, p. 49, pl. ii c, iii B, text-figs. 8 B-D, G, K; 10 C-J; 11 A-C.
- ?1957 *Hoegia autevsiana* Townrow, p. 50, pl. iii c, text-figs. 8 E; 9 L; 10 K; 11 D.

Description. This is the most frequent species in several beds of the Ischigualasto Formation. It is also present in association with all *Rhexoxylon* stems. The better fragments show the forking of the main rachis (Frenguelli 1944, pl. iv, pl. vii, 1), but since the whole leaf is large, small specimens appear bipinnate or simply pinnate. The size, and especially the shape of the pinnules are the most important characters of the species; usually the pinnules are rhomboidal or somewhat square, with slightly contracted bases and the distal margin may be entire or irregularly lobed. The pinnules of one row may overlap or be separated. Elongated pinnules do occur, but they are not common, their shape being slightly falcate. Venation is also characteristic; one or more groups of veins arise at the base of the pinnule from the rachis, each vein forking usually once or twice and curving slightly towards the lateral margins. Commonly the veins tend to concentrate all in one basiscopic point. Our specimens are in complete agreement in size, shape, and venation with the material described by Frenguelli as *Zuberia zuberi* and also with Townrow's *Hoegia papillata*. By transparency a distinct border is seen along the margins of the pinnules, devoid of venation and inner coaly substance.

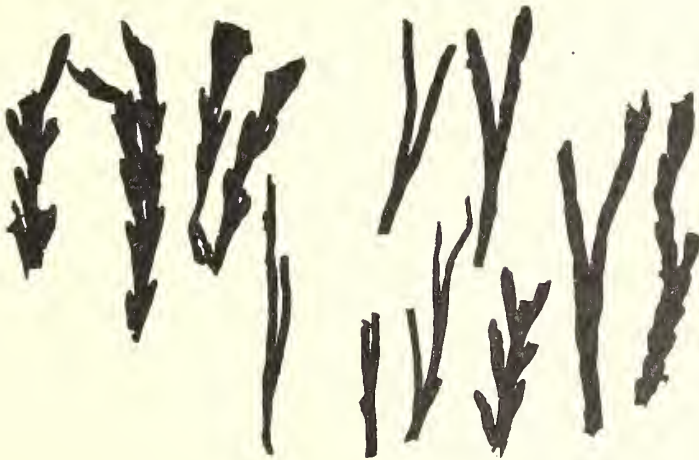
One cuticle is slightly thicker than the other; both are very thick (about 8 μ). Epidermal cells on both cuticles are typically isodiametric and polygonal, with straight walls, about 50-60 μ . Cuticular projections from anticlinal walls present; they are most irregular in their thickness. Short, round papillae are commonly found on the cell surface (more frequent on the thicker cuticle). The stomata are indistinctly orientated, present on both cuticles and evenly distributed, rarely with subsidiary cells in contact. There are about 70-110 stomata per square millimetre. The stomatal apparatus is typically monocyclic, circular to oval. The guard cells are sunken in a pit formed by 4-6 subsidiary cells which coalesce around the mouth of the pit, forming usually a strong rim of cutine. Subsidiary cells normally not papillate (but sometimes they are).

The papillae are sometimes almost absent on a whole cuticle; or they may vary greatly in concentration over the same cuticle. It seems that this is a variable character. The papillae are usually small and solid.

Material studied. San Juan Province, Ischigualasto Basin. Bed 1: LP 7449, 7450, 7453; LIL 2768, 2769. Bed 2: LP 7451, 7454; LIL 2770. Bed 3: LP 7439, 7440-3; LIL 2767, 2772. Bed 4: LP 7430-4,



a



b



c

TEXT-FIG. 1. Compressions of *Dicroidium* leaves, $\times \frac{3}{2}$. a, *D. zuberi* (Frenguelli) Archangelsky; slide LP 425, fragmentary pinnae. b, *D. elongatum* (Carruthers) comb. nov. (the four central linear pinnae), and *D. coriaceum* (Johnston) Townrow; slide LP 427 shows extreme types and transitional forms between the two species. c, *Dicroidium* sp.; slide LP 428, fragmentary pinnae.

7436-8, 7441, 7448; LIL 2765, 2776. Bed 7: LP 7452. Slides LP 417, 424, 425; LIL 504-8. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Frenguelli (1944) described four species of his previously established genus *Zuberia*. Two of the species, *Z. sahnii* and *Z. barrealensis*, based on very fragmentary material. *Z. zuberi* and *Z. feistmanteli*, as far as the Argentinian material is concerned, are very similar and there are no important characters differentiating them. *D. feistmanteli* (Johnston) Gothan, is distinguished by the entire margins of its pinnules, less crowded veins, much thinner cuticle and fewer stomata (25 against 70-100 per mm. in *D. zuberi*).

The Ischigualasto specimens, though fragmentary, are identified with Frenguelli's material (which I have examined in the La Plata Museum Collection) because they agree in size, shape, and venation of pinnules. Moreover, Frenguelli's four species integrate in these respects and for this reason I have merged them all in *D. zuberi*.

The original specimen (type) of *Zuberia zuberi* is the one that Szajnocha described as *Cardiopteris zuberi* (from Argentina) and Frenguelli combined in his genus *Zuberia*. This specimen should therefore be the holotype, but I do not know where it is located, and Szajnocha gave no collection reference or numbers in his paper (1888). I select a neotype, LP 9520, a large leaf with a main bifurcate rachis (figured by Frenguelli 1944, pl. iv).

Our material also coincides in morphology and cuticular structure with that described as *Hoegia papillata* by Townrow. As *D. zuberi* has a forked main rachis of leaves, there is no reason to keep a different species for pinnate fragments, which are too small to show the main rachis of the whole leaf.

Some specimens (particularly those found in Bed 2) present a very thick cell border of the pinnules, resembling in this respect *Hoegia antevsiana* Townrow. I suggest that Townrow's species might be regarded as a mere variation of *D. zuberi*, because they coincide in stomatal structure and the size of epidermal cells.

Dicroidium elongatum (Carruthers) comb. nov.

Plate 97, figs. 1, 3; Plate 98, fig. 4; text-fig. 1b, 2a

1872 *Sphenopteris elongata* Carruthers, p. 355, pl. 27, fig. 1.

1943 *Xylopteris elongata* (Carruthers) Frenguelli, p. 318, text-figs. A, B.

1962 *Xylopteris elongata* (Carruthers) Frenguelli; Townrow 1962, p. 123.

Description. The Ischigualasto material is comparable in shape and size with the lectoparatype figured and described by Townrow (1962b), having very elongated segments which sometimes fork dichotomously. The segments are almost parallel-sided and taper very gradually to a short but rounded apex. The best specimens are fairly

EXPLANATION OF PLATE 97

Figs. 1, 3. *Dicroidium elongatum* (Carruthers) comb. nov. 1, Specimen showing bifurcation of the main rachis; LP 7456, $\times 1$. 3, Two stomata; LP 416, $\times 300$.

Figs. 2, 5. *D. coriaceum* (Johnston) Townrow. 2, Fragment of leaf showing bifurcate rachis; LP 7457, $\times 1$. 5, Two stomata; LP 437, $\times 300$.

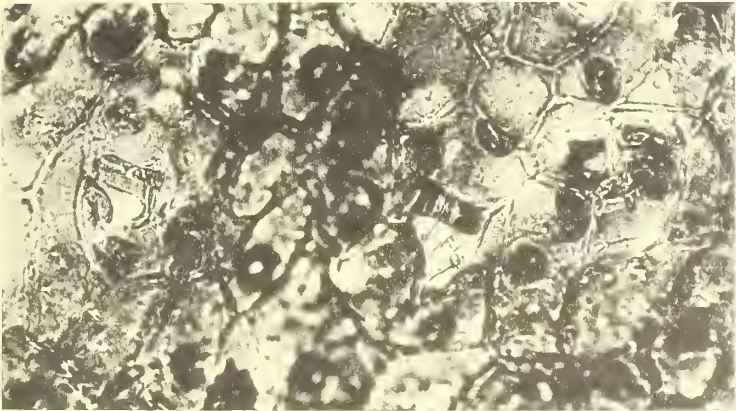
Fig. 4. *D. sp.*, a few stomata showing papillae overhanging the mouth of the pit; LP 432, $\times 300$.



3



1



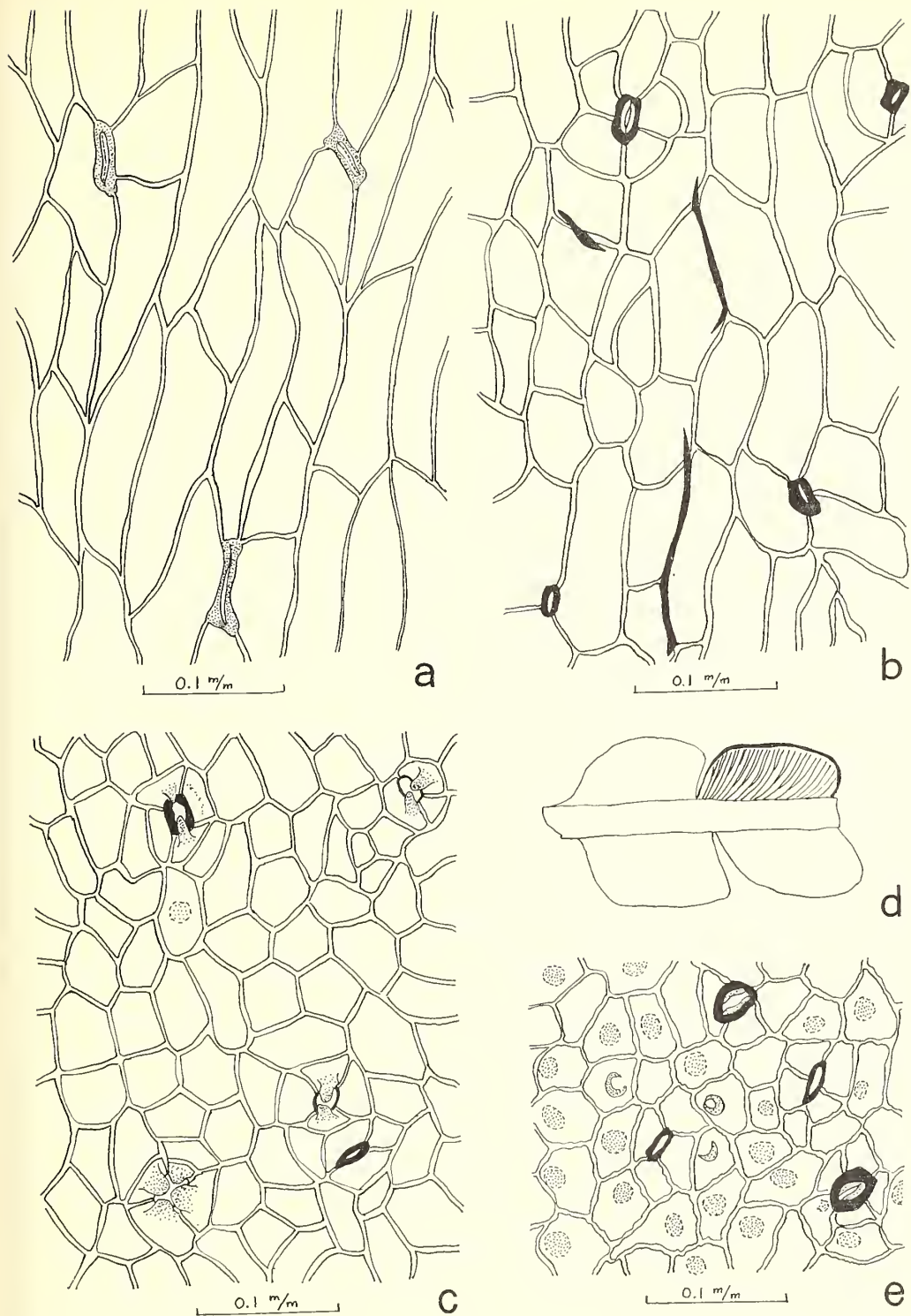
4



5



2



TEXT-FIG. 2. Drawings of *Dicroidium* leaves. *a*, *D. elongatum* (Carruthers) comb. nov.; epidermis showing three stomata, slide LP 14. *b*, *D. coriaceum* (Johnston) Townrow; epidermis showing stomata and cuticular ridges, slide LP 437. *c*, *D. sp.*; epidermis showing stomata and papillae overhanging the mouth of the pit, slide LP 432. *d*, *D. zuberi* (Szajnocha) comb. nov.; outline of pinnules showing venation, slide LP 425; $\times 1.5$. *e*, As last, epidermis showing stomata and papillae on cells, slide LP 418.

complete, and they are preserved as impressions; compressions are usually very fragmentary, represented by only the single linear segments. Though a midrib is not at first visible in these segments, a suggestion of one is visible when the fossil (consisting of little more than cuticles) is cleared as a transparency. Also by transparency a clear marginal zone may be seen, with no coaly substance in it. Some fragments of pinnae seem to have wider segments, showing what may be an incipient marginal lobing. Such fragments show, by transparency, a clear median vein.

The cuticles may be of equal thickness, or one (which Townrow regards as the lower) is rather thinner. The epidermal cells on both cuticles are alike, usually rectangular or elongated, with their longitudinal axis parallel to the long axis of the segments. They form ill-defined rows. Isodiametric epidermal cells also do occur. Long cutin ridges are present on both cuticles, and they are also longitudinally orientated, although oblique and transversely orientated stomata have been observed. They are widely separated and rarely have subsidiary cells in contact. I have counted about 10–15 stomata per square millimetre. Epidermal cells are $100\text{--}150\text{ }\mu$ long $\times$ $20\text{--}40\text{ }\mu$ wide (and $50\text{--}70\text{ }\mu$ when isodiametric). Their outline is straight, showing small sinuities due to different thickness of the anticlinal walls. Papillae are rarely seen. The stomatal apparatus is oval, typically monocyclic. The guard cells are feebly cutinized and are sunken in a pit formed by 4–6 unspecialized subsidiary cells. The mouth of the pit usually has a distinct cutin border, sometimes forming a continuous rim. The poles of the guard cells are sometimes exposed on the surface. Occasionally, a circular stomatal apparatus was seen, with strongly sunken guard cells. In the apical parts of the segments, the epidermal cells tend to be more isodiametric.

Material studied. San Juan Province, Ischigualasto Basin. Bed 2: LP 7451; Bed 4: LP 7429, 7438; LIL 2766. Bed 6: LP 7418–28; LIL 2763, 2764, 2771. Bed 7: LP 7452, 7456, 7463, 7464, 7466. Slides LP 412–16, 426, 427; LIL 501–3. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Our material agrees in all respects with the type material of *D. elongatum* as described by Townrow (1962b), in the shape and size of the segments and in the cuticular structure.

In Ischigualasto, *D. coriaceum* and *D. elongatum* occur together in some beds, while *D. elongatum* is found alone in some others (Beds 4 and 7).

In the Barreal region (San Juan Province) three plant beds have been recognized (Bonetti 1963). *D. elongatum* does occur together with *D. coriaceum* in Bed I, but in Bed II, *D. elongatum* occurs alone.

In some other Triassic localities in Argentina, *Xylopteris* species have been described, but there is no mention of the *Johnstonia* type of leaves (Neuquen, Santa Cruz, etc.).

All these additional references seem to indicate that *D. coriaceum* and *D. elongatum* are probably two different species, although they have some morphological similarities.

Dicroidium coriaceum (Johnston) Townrow

Plate 97, figs. 2, 5; Plate 98, fig. 3; text-figs. 1b, 2b

Description. The leaf is very variable. The less-lobed segments (pinnae) are somewhat similar to the *D. elongatum* linear segments, although they are wider. The lobing of the

segments (differentiation of the pinnules) may be just incipient, or it may be quite developed; in such a case, the resulting pinnules may be again similar to unlobed pinnae. All three degrees of variation have been observed in the abundant material. The size and the shape of the Australian material described by Townrow (1957) may be matched in our specimens. The pinnules of the well-developed pinnae are linear and have rounded apices. The segments are bordered by a rim of cutin, clearly seen by transparency. One vein penetrates each segment, and it may fork once or twice (veins were seen by transparency).

Both cuticles are of a similar thickness. The epidermal cells are of two kinds: elongated (more than $100\ \mu$ long $\times$ $40\ \mu$ wide) and isodiametric (50 – $70\ \mu$ in diameter). Low cuticular papillae, one per cell, are sometimes seen. The stomata are usually longitudinally orientated, sometimes obliquely or transversely. The walls of epidermal cells are straight, sometimes with irregular cutinization of anticlinal walls. Strong longitudinal ridges of cutin are also present. The stomata are irregularly disposed, separated and never with subsidiary cells in contact. There are about 30 stomata per square millimetre. The stomatal apparatus is typically imperfectly dicyclic, with feebly cutinized guard cells, little or not at all sunken. There are 4–6 subsidiary cells, the polar usually differentiated from the lateral. Subsidiary cells often having papillae. When the guard cells are little sunken, the subsidiary cells (usually the lateral) form a rim of cutin at the opening of the epistomatal chamber.

Material studied. San Juan Province, Ischigualasto Basin. Bed 6: LP 7424, 7425, 7428; LIL 2764, 2771. Material Romer, LP 7457, 7458, 7460–2, 7465. Slides, LP 426, 427, 436, 437 (Bed 2); LIL 515. Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. Our material seems to have more variation in cuticular structure than that described by Townrow. However, Australian specimens are very fragmentary, while our material presents a wide variety of leaves and different segment types. I believe that epidermal cells tend, in this species as a rule, to be longitudinally orientated in long pinnae or pinnules. Townrow's material shows only short, not fully developed pinnules, where the epidermal cells are usually more isodiametric. The papillae may be fairly common or may be lacking in large sectors of leaves; it is also a very variable character.

Extreme types of *D. elongatum* and *D. coriaceum* are quite distinct in shape. Intermediate forms can, however, be confused, and their determination becomes more or less arbitrary. The cuticles of both species are alike. The elongation of epidermal cells depends on the shape of segments and pinnules. Similar segments of both species have similar epidermal cells. Papillae are more abundant in *D. coriaceum*, but they are also present, though rarely, in *D. elongatum*. Stomata are similarly orientated in both species, and their concentration is alike. The structure of the stomatal apparatus is similar, though in *D. elongatum* guard cells seem to be more sunken. Differentiation of polar and lateral subsidiary cells is more clear in *D. coriaceum*.

It is difficult and may even be arbitrary to distinguish these species, for there are intermediate types. The cuticular structure is of no particular help in this respect. It seems, however, wise to have the two forms separated into two species. Certainly there are no firm grounds for the use of separate genera.

Dicroidium sp.

Plate 97, fig. 4; text-figs. 1c, 2c

Discussion. Although there is a lack of certain characters, particularly the gross morphology of the fronds, this species is described here in order to complete the presentation of all the taxa which are found in association with the petrified *Rhexoxylon* stems. The only exception is *Neocalamites*, which is found with these compressions but which cannot be related to either *Dicroidium* or *Rhexoxylon*.

Description. This species is the least frequent in Ischigualasto. The size and the shape of pinnules and pinnae coincides with *Dicroidium superbum* (Shirley), as described by Townrow (1957). Pinnules are usually longer than wider, and their margins are sinuous or lobed. One complete pinna shows a narrow acute apex. Usually one decurrent vein was seen by transparency, running up to near the apex of the pinnule. Forking of veins was not clearly seen, but it may be possible in larger pinnules. By transparency the pinnules show a clear border of cutin without coaly substance.

Both cuticles are of an even thickness. Epidermal cells are usually isodiametric, except on the rachis and on the main vein, where they tend to be rectangular or elongated. Anticlinal walls are straight. On the surface, single round papillae are sometimes seen; one, rarely two, per cell. The stomata are irregularly orientated and distributed, sometimes with subsidiary cells in contact. The stomatal apparatus is usually oval, sometimes subcircular, imperfectly dicyclic. The guard cells are cutinized and sunken in a pit formed by 4–7 subsidiary cells, which can be wedge-shaped or of irregular shape. Subsidiary cells each bearing characteristically one round or slightly elongate papilla. Papillae usually overhanging mouth of pit, almost closing it. Guard cells slightly thickened near the aperture. Polar and lateral subsidiary cells not differentiated.

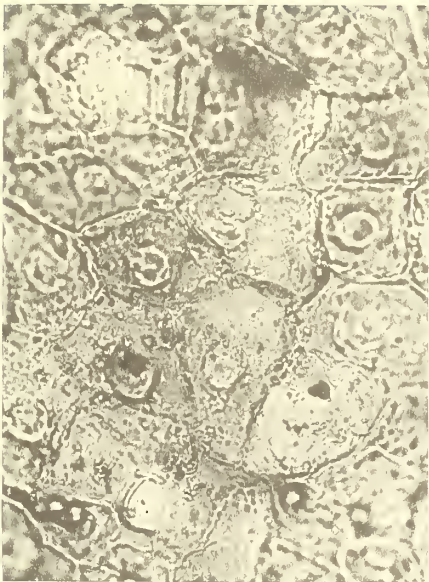
A few large pinnules are included in this species. In gross morphology they resemble *D. zuberi*, but they differ in their stomatal structure, and in the presence of strongly developed papillae and unicellular hairs. The cuticle of these pinnules is thick, up to 10 μ (one of the two is slightly thinner); the epidermal cells are isodiametric, often square or rectangular, forming definite longitudinal rows for a variable distance, about 40–50 μ in diameter, when elongated up to 60 μ long $\times$ 20–30 μ wide. Epidermal cells as a rule bear one strong, usually hollow, papilla; towards the margins papillae becoming high, in some cases resembling unicellular hairs up to 50 μ long. Cell walls with a uniform thick border. Stomata present on both cuticles, up to 60 per square millimetre. Stomata slightly sunken, surrounded by 4–5 subsidiary cells. Mouth of pit square, rectangular sometimes oval. Normally, subsidiary cells with strongly developed papillae overhanging the mouth of the pit, sometimes almost closing it. Epidermal cells on rachis, elongated and bearing papillae. Longitudinal cutin ridges also present.

EXPLANATION OF PLATE 98

- Figs. 1, 2. *Dicroidium zuberi* (Szajnocha) comb. nov., LP 418. 1, Epidermis showing distribution of stomata, $\times 120$. 2, Epidermal cells with papillae and two stomata, $\times 300$.
Fig. 3. *D. coriaceum* (Johnston) Townrow, LP 437; epidermis with thickened bands of cutin, $\times 120$.
Fig. 4. *D. elongatum* (Carruthers) comb. nov., LP 416; epidermis, $\times 120$.



1



2



3



4

There are variations: some pinnules although having stomata with protective papillae, have no papillae on ordinary epidermal cells. Sometimes, most stomata are devoid of protective papillae, but after careful search, a few are found to be present.

It is difficult to establish whether these specimens are merely ecological varieties of *D. zuberi* or if they do belong to another species.

Material studied. San Juan Province, Ischigualasto Basin. Slides LP 428–35; LIL 509–15 (Beds 1, 3, 4, 6). Age: Middle to Upper Triassic, Ischigualasto Formation, Agua de la Peña Group.

Discussion. The size and the shape of the small pinnae resemble *D. superbum* (Shirley) Townrow. However, the cuticle shows some differences, mainly in the stomatal apparatus. No papillae overhanging the stomatal pit are known in *D. superbum*. Such papillae are normal in *Lepidopteris* but for other reasons our leaves must be placed in *Dicroidium*. The rachis of our specimens is not covered by lumps; the shape of the pinnules is not alike (neither is the venation) and the stomatal apparatus is not circular as a rule but often tends to be oval. On the other hand, similar stomata have been reported and figured by Townrow for *D. odontopteroides* (1957, figs. 5D, 6M).

As our material is scanty, I prefer to make no specific assignation until better specimens become available from this and other Triassic localities.

ASSOCIATION OF *DICROIDIUM* LEAVES AND *RHEXOXYLON* STEMS

San Juan Province, Ischigualasto Basin.

The material described here was collected from about 10 lenses of plant-bearing sandstones, over a distance of about 4 km. There are also compressions of *Neocalamites* stems. No other compressions have so far been found in these particular beds, although in other strata of the formation there are different plant elements. There are several petrifications in close association with the compressions; most of them belong to *Rhexoxylon*. One small petrification belongs to a Cycad-like stem, *Michelilloa waltonii* Arch. and Brett (1963), which is unlikely to have borne *Dicroidium*, because the leaf base scar is too small. Finally, one petrified Conifer was recently described as *Protojuniperoxylon ischigualastensis* Bonetti (1966), which is also unlikely to have borne *Dicroidium* leaves. The overwhelming abundance of *Rhexoxylon* as petrification, and *Dicroidium* as compression, provides strong support of probable relationship.

San Juan Province, Barreal

In the locality Quebrada de la Tinta, La Cortaderita Formation, Bed III. 36 (Bonetti 1963), also of Triassic age, some *Rhexoxylon* petrified stems have been found. They have not yet been described, but Dr. Bonetti who collected them, kindly showed the material to me. It undoubtedly belongs to *Rhexoxylon*, and possibly to the Ischigualasto species *R. piatnitzkyi*. In the same bed, Bonetti reports the following plant impressions: *Dicroidium lancifolium* and *D. feistmanteli* (which in her sense is equivalent to *Zuberia zuberi* of Frenguelli) and *Pseudecten ctenophylloides* as the most abundant; less abundantly are found *Cladophlebis mendozaensis*, *Dicroidium narrabeenense*, and *Pteruchus dubius*. Therefore, there are four of the six species belonging to the *Dicroidium*

complex, two of them being dominant. *Cladophlebis*, being a fern, is not related to *Rhexoxylon*. Only *Pseudoctenis* could perhaps be related to the petrified stems, apart from *Dicroidium* species.

South Africa

In South Africa the evidence of association is less clear, the facts not being available to me. Species of *Rhexoxylon* certainly do occur in the same formations with *Dicroidium* leaves. The stratigraphic references as given by Walton (1956) and Du Toit (1954) indicate that *Rhexoxylon* is present in several localities; all findings of the stems are referred to the Triassic Molteno and Red Beds in the Cape Province, and to the Somabula Beds of Rhodesia. Both units are part of the Stormberg Series. In the Red Beds, only silicified woods of *Rhexoxylon* and *Dadoxylon* are known. In the Molteno Beds, a large number of leaf impressions are known, including several species of *Dicroidium*. But in the taphoflora of the Somabula Beds in Rhodesia, apart from *Rhexoxylon*, three species of *Dicroidium*, one of *Taeniopteris* and one of *Schizoneura* have been reported. So, again only two genera can be related to *Rhexoxylon*, and the more important of them, having several representatives, is *Dicroidium*.

Resuming all the facts, *Rhexoxylon* is always associated with *Dicroidium* in two localities of Argentina and in two of South Africa. In Ischigualasto, they are the only taxa which might be related. In two other localities (Barreal, Argentina and Rhodesia, South Africa) *Rhexoxylon* and *Dicroidium* are almost exclusive elements in association, apart from *Pseudoctenis* in one and *Taeniopteris* in the other. Therefore, all four plant associations from South Africa and Argentina are consistent with the idea that *Rhexoxylon* bore *Dicroidium* leaves.

Further evidence is needed for making a much better case of this association. We are not able at present to relate particular species of *Dicroidium* leaves with species of *Rhexoxylon*. Indeed, different species of *Rhexoxylon* may represent different stages of development of one stem. An organic connexion is therefore needed.

STRUCTURAL RELATION OF *DICROIDIUM* AND *RHEXOXYLON*

On general grounds *Rhexoxylon* may be related in its structure to some Palaeozoic pteridosperms (Medullosae; Archangelsky and Brett 1961). On the other hand, all other organs of *Dicroidium* (male and female fructifications) are also related to the Palaeozoic pteridosperms. The leaves are also related to the pteridosperms as they have a fern-like appearance, with dichotomous main rachis and a thick cuticle with specialized stomata. It may be added that there is agreement between the leaf base of *Dicroidium* and the scars on *Rhexoxylon*, but only in their similar size and shape, for we have no supporting evidence of the vascular bundles.

The geological and geographical distribution shows *Rhexoxylon* and *Dicroidium* confined to the Gondwana Palaeofloristic Region, during the Triassic Period. Therefore, the data so far available are not against considering these two taxa as belonging to the same plant. The peculiar structure of *Rhexoxylon* is not in favour of its abundant representation in the sediments.

CONCLUSION

This paper makes a strong suggestion that the *Dicroidium* leaf was borne on the *Rhexoxylon* stem, but I do not claim that the present evidence constitutes overwhelming proof. It is merely circumstantial evidence, each item no more than suggestive, but gaining greatly in weight by repetition. I publish this idea mainly in the hope that it will cause others to notice further evidence bearing on this question. On the assumption that the idea is right, I examine some of the taxonomic consequences.

The Corystosperms constitute an important stock of information. Several Mesozoic groups, such as the Peltaspermaceae and the Caytoniaceae may be linked with them in varying degree. The Corystosperms are obviously an evolutionary step forward from the Palaeozoic pteridosperms, and attention should be paid to them when new relationships are to be established with other Mesozoic pteridosperms. Dispersed information available at present, seems to indicate that the Mesozoic pteridosperms played an important role not only in a particular palaeogeographical area, but all over the world. The stems of *Hernanophyton* from the Jurassic of U.S.A., *Pteroma* and *Pachypteris* (Harris 1964) from the Jurassic of England, and even the Peltaspermaceae, clearly indicate the world-wide occurrence of plants whose allies are the Palaeozoic pteridosperms.

Finally, I believe that further research work with the Mesozoic pteridosperms is of utmost importance for Palaeobotany, not only to establish the real taxonomic status of the different groups, but also to look for further evidence in relation to the origin of the angiosperms, which are claimed as descendants of the pteridosperms.

Acknowledgements. I express my gratitude to Professor Thomas M. Harris (Reading University) who encouraged this work, and supplied an important source of information. I am indebted to Dr. Alfred Romer for his kindness in offering for study the plant material collected during the 1964–1965 La Plata–Harvard Expedition to Ischigualasto.

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SERGIO ARCHANGELSKY
Research Fellow
National Research Council,
Museo de Ciencias Naturales,
La Plata,
Argentina

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ASTROCYSTITES DISTANS SP. NOV., AN EDRIOBLASTOID FROM THE ORDOVICIAN OF EASTERN AUSTRALIA

by B. D. WEBBY

ABSTRACT. A new Ordovician edrioblastoid, *Astrocystites distans* sp. nov., and other miscellaneous pelmatozoan plates are described from the lower part of the Cliefden Caves Limestone WNW. of Mandurama, New South Wales. The edrioblastoid is similar to the only other species of *Astrocystites* known, *A. ottawaensis* Whiteaves from the Trenton Limestone of Ottawa, which was hitherto the sole representative of the group. This represents the first record of an edrioblastoid outside North America. Sections of the Australian material have revealed details of internal structures not previously known in the group.

DURING recent geological work in the Lower Palaeozoic successions of the central-west of New South Wales by G. H. Packham and the writer, an abundance of pelmatozoan material was found in a band of fawn-grey thinly bedded limestones. Unfortunately virtually all of it is fragmentary, consisting mainly of stem ossicles, incomplete thecae and disarticulated plates. The thecae and plates form the basis of this paper. The band of limestones also contains polyzoans, brachiopods, corals, gastropods, trilobites, and nautiloids, and lies within the lower thinly bedded part of the Cliefden Caves Limestone. The localities from which the collection was made are situated on the property of Boonderoo, about $\frac{1}{4}$ mile ESE. of the entrance to Cliefden Caves (Bathurst sheet, 1:250,000; S155-8, Edit. 1-AAS, Series R 502; Grid ref. 186848), and near Little Boonderoo (Grid ref. 186844).

The stratigraphy of the area was described by Stevens (1952), but the faunas have received little attention. Some of the corals in the Cliefden Caves Limestone were described by Hill (1957) and suggest a Trenton age. However, the presence of graptolites, probably of the *Nemagraptus gracilis* zone, in the overlying shales and limestones of the Malongulli Formation (Sherrard 1954) implies an older age. The faunas are being studied by Packham and the writer, and it is hoped to offer a more exhaustive statement on the age and correlation of units in the succession.

SYSTEMATIC DESCRIPTION

The registration numbers of specimens in the University of Sydney, Geology Department, palaeontological collections have the prefix USGD.

Subphylum PELMATOZOA Leuckart 1848

Class EDRIOBLASTOIDEA Fay 1962

Family STEGANOBLASTIDAE Bather 1900

Genus ASTROCYSTITES Whiteaves 1897 (= STEGANOBLASTUS Whiteaves 1898)

Type species. *Astrocystites ottawaensis* Whiteaves.

[Palaeontology, Vol. 11, Part 4, 1968, pp. 513-25, pls. 99, 100.]

Nomenclature and previous work. Whiteaves (1897) first described *Astrocystites ottawaensis* from the Trenton Limestone of Ottawa. In the same year Bather raised objections to Whiteaves's generic name on the grounds of possible confusion with *Asterocystis* Haeckel, and suggested that Whiteaves substitute the name *Steganoblastus*. The new generic name was introduced by Whiteaves (1898), and the family name Steganoblastidae of the Class Edrioasteroidea added by Bather (1900). Whiteaves's original generic name, *Astrocystites*, was restored by Bassler (1935) on grounds of priority, and he introduced a new family name, Astrocystitidae, to replace Steganoblastidae. However, since Steganoblastidae, which is based on a junior objective synonym, has priority and has been a more widely used name, it would seem desirable that it be retained. This view accords with Art. 40 of the International Code of Zoological Nomenclature.

Astrocystites was interpreted as an edrioasteroid by Bather (1914*b*), and as a blastoid by Hudson (1925). Bassler (1935, 1936) also classified the genus in the Edrioasteroidea, but observed that, since only a few specimens are known and pending further discoveries it might well be assigned to the Protoblastoidea. Fay (1962) contended that it did not belong either to the edrioasteroids or the blastoids, and raised a new class, the Edrioblastoidea, to accommodate it. He noted its resemblances to blastoids in having five petaloid ambulacra with pores between ambulacral plates, five radials, five deltoids, five orals, and a primitive stem, and its differences in exhibiting five basals, numerous infradeltoids, a hydropore, and deep infolds in plates of the theca. His reasons for removing *Astrocystites* from the edrioasteroids are not clearly stated. Judging from Bather's and Fay's descriptions of *A. ottawaensis* it is evident that there are close similarities with edrioasteroids, especially in the nature and arrangement of floor and cover plates, and pores in the ambulacral areas, and in the presence of a cluster of small plates around the anal opening and hydropore. The genus may be distinguished from edrioasteroids by having a pyriform theca, a stem, five basals, five radials, and five deltoids. Regnéll (1966, p. 150) preferred a non-committal term 'third aperture' for the structure usually referred to as the hydropore in edrioasteroids, because it may alternatively be interpreted as a gonopore or a hydrogenopore. In the following account of the new edrioblastoid, the term hydropore has been retained, although it is recognized that the aperture may also have acted as an outlet for sexual products.

The original descriptions of *Astrocystites ottawaensis* by Whiteaves (1897) and Bather (1914*b*) were based on three complete specimens. However, Wilson (1946) and Fay (1962) indicated that only one specimen is now known to exist, the others having been misplaced or lost. Wilson listed the specimen from the Cobourg beds, in Booth Street, Ottawa, the topmost unit of the Ottawa Formation, and of Trenton age. Fay founded the Class Edrioblastoidea on this single remaining specimen. Details of the internal structures remain unknown, yet there seems to be no good reason why this should be so, for Spencer (1938, p. 291) observed that the Trenton rocks of Ottawa contain beds 'composed almost entirely of separate ossicles of species of *Steganoblastus*'; Bassler and Moodey (1943, p. 197) listed *A. ottawaensis* from three different localities and horizons, namely, from the Upper Trenton *Hormotoma trentonensis* beds of Ottawa, from the Hull Limestone of Kirkfield, Ontario, and from the Curdsville Limestone of Mercer County, Kentucky. From these statements, it would, therefore, be surprising if no other material is available either in existing collections or in outcrops. It is to be hoped that further material will be found, and sections cut in order to elucidate the

nature of the internal structure of *A. ottawaensis*, enabling closer comparisons to be made with the fragmentary Australian material.

The writer has reservations about the need to separate *Astrocystites* from the Edrioasteroidea and to erect a new class, the Edrioblastoidea (Fay 1962). Even greater doubt is felt about the assignment of edrioasteroids and edrioblastoids to different subphyla (Fell 1965; Fell and Moore 1966). Although Fay's classification has been followed, the obvious morphological similarities of *Edrioaster* and *Astrocystites*, the appearance of *Astrocystites* in the Middle Ordovician during the period of maximum diversification of the edrioasteroids, and the presence of several forms with comparable sac-like form and straight ambulacra (e.g., *Cystaster* and *Cyathocystis*) still regarded as edrioasteroids (Regnéll 1966), support the view that edrioblastoids should be grouped in an order or a suborder of the Class Edrioasteroidea.

Astrocystites distans sp. nov.

Plate 99, figs. 1–10; Plate 100, figs. 1–8; text-figs. 1–4

Diagnosis. A species of *Astrocystites* with slit-like ambulacral pores, averaging 25–30 per cm., and small, circular hydropore.

Material. Two partially complete specimens (holotype, USGD 2302, and paratype A, USGD 2303), five incomplete specimens showing sections across the theca (paratypes B–D, USGD 2309; other paratypes, 2304–6, 2312, 3303), two serially sectioned specimens (paratypes, USGD 2310–11) and plate fragments (paratypes, USGD 2308, 2313–14). All the type specimens come from the lower part of the Cliefden Caves Limestone $\frac{1}{4}$ mile ESE. of the entrance to Cliefden Caves, excepting USGD 3303, which is from the same horizon near Little Boonderoo.

Description. Theca medium-sized, incompletely preserved. Holotype (USGD 2302) measures more than 18 mm. in height and 20 mm. in width; paratype A (USGD 2303) is more than 23 mm. high and 25 mm. wide. Base of theca not observed. Basals small, convex plates with strong radial crenulations and small apical openings (probably caused by wear on this more prominent part of the plate); basals 3–6 mm. wide and 2.5–5 mm. in height. Radials large, subpentagonal, estimated to be 8–14 mm. wide and of similar height; lower and lateral parts exhibit gentle to deep crenulations, seemingly at right angles to sutures, and upper medial part of plate underlies distal end of each ambulacrum. Small, tightly fused infradeltoids appear to be represented in posterior interradius around possible anal opening of holotype. These have also been seen in other interradii in cross-section. Deltoids large, subtriangular, thickened plates, approximately 5–8 mm. in both height and width, and with deep to undulating crenulations on external surface. Hydropore circular, 0.5 mm. in diameter, situated near apex of posterior interradius.

Straight petaloid ambulacra; in holotype ambulacrum 15 mm. long and 6 mm. wide, and in paratype A, more than 22 mm. long and 6.5 mm. wide; ambulacra gently curved around theca in distal and medial regions, but more strongly arched and thickened in proximal region leading to mouth; ambulacral groove bounded by row of floor plates on either side, and united by very close suture; individual floor plates cannot be differentiated, owing to extreme fusion of plates and nature of preservation; regularly spaced, slit-like pores extend along each row of floor plates, about 25–30 per cm., and become

smaller and more closely spaced proximally. It is also virtually impossible to recognize junctions between floor plates and deltoids because of the complete fusion and crystallographic continuity of calcite in the plates; they can seldom be distinguished even in thin sections under a polarizing microscope. In the distal part of the ambulacrum pores pass through floor plates into a canal lying between the radial and the floor plates; it presumably opens into the thecal cavity at the top of the radial. Floor plates in proximal part of ambulacrum and margins of deltoids are thickened, producing an inwardly directed flange-like extension through which pores penetrate and communicate with the thecal cavity. Flanges seem to form part of the frame surrounding the peristome.

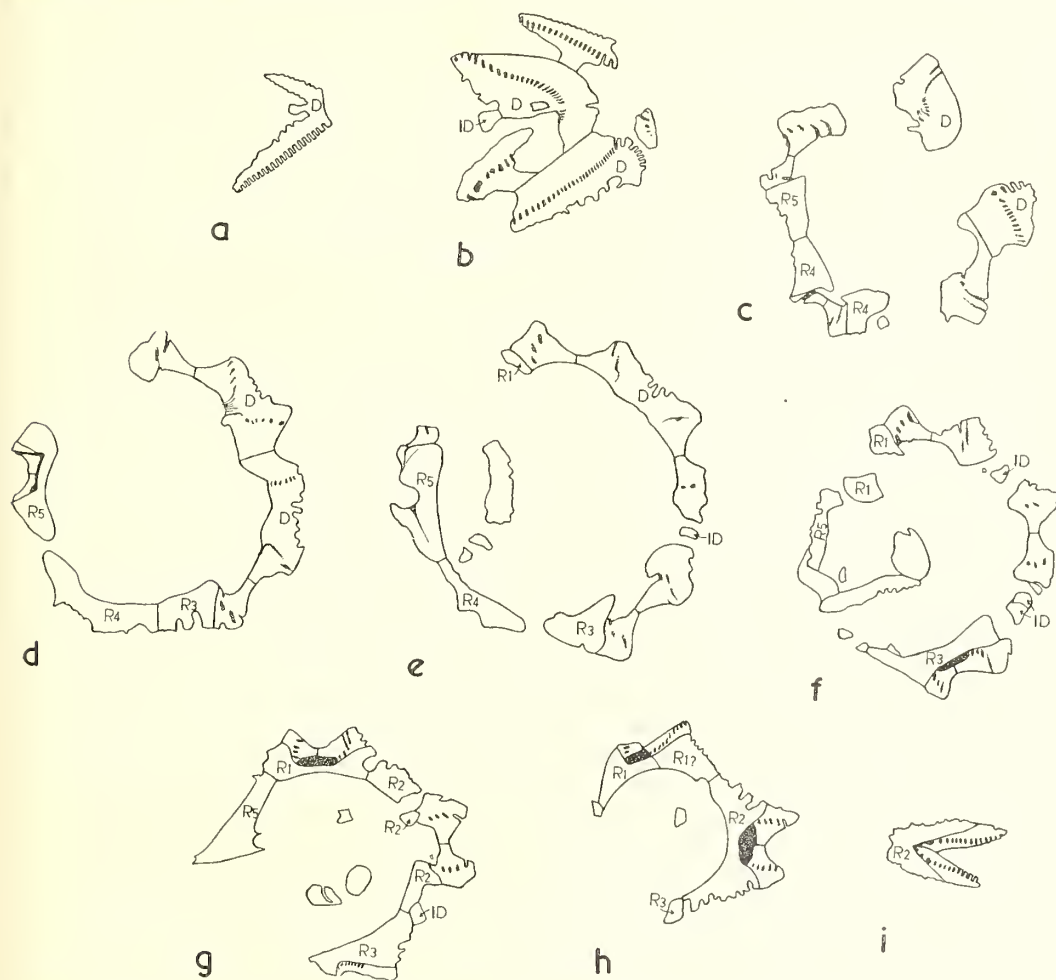


TEXT-FIG. 1. *Astrocystites distans* sp. nov. *a*, longitudinal section of paratype B, USGD 2309, $\times 5$, showing large, vertical interradiar element and the nature of the pores inside the theca. The circum-oral ring of the water vascular system may have crossed the element in the lower part, below the level of adjacent pores. *b*, oral view of holotype, USGD 2302, $\times 5$, showing right postero-lateral ambulacrum and posterior interradius with hydopore. At the top of the ambulacrum there is a plate which may be interpreted as a radial element in the frame, or a foreign plate fragment lying inside the peristome.

Larger vertical interradiar elements are found in the angles between floor plates and adjacent radii, and make up the interradiar component of the frame (text-fig. 1*a*); the upper part of the interradiar element is smooth and may have been connected in the frame, but the lower part, just below the level of adjacent pores, is irregular, and may have been free. Floor plates on either side of the interradiar element are apparently narrower and taper inwards, as associated pores are smaller and slope obliquely in towards larger vertical canals on either side of the interradiar element. Structure interpreted as stone canal extends from the interior in an adoral direction between interradiar element of the posterior interradius and left posterior ambulacrum. From the interior a narrow canal expands into a double chamber, which is linked by a narrow obliquely inclined canal to a funnel-shaped chamber (Pl. 100, fig. 3). It opens to the exterior by the centrally placed hydopore. A radial element is suggested from the oral region of the holotype (text-fig. 1*b*) but it has not been confirmed in other specimens. Cover plates and oral plates have not been observed. Tiny pits scattered on the external surface of parts of the theca possibly represent attachment points for small spines.

A series of cross-sections, unfortunately slightly oblique, was prepared from paratype USGD 2310; the specimen is fragmentary, lacks basals, and a prominent joint inter-

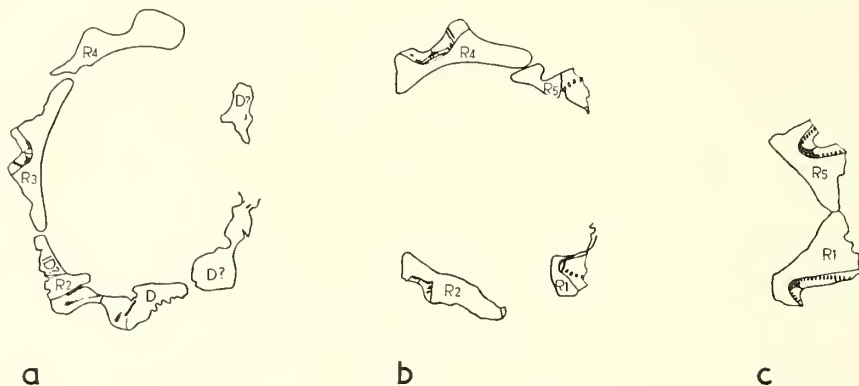
sects one side of the theca, resulting in recrystallization and disruption of plates. Radials, deltoids, infradeltoids, and floor plates are represented (text-fig. 2). Pores, although mainly cut obliquely, appear to extend through floor plates along the length of the ambulacra, and canals between radials and floor plates are clearly exhibited in the distal parts of ambulacra (text-fig. 2*f-h*).



TEXT-FIG. 2. *Astrocystites distans* sp. nov. Slightly oblique cross sections of paratype, USGD 2310, $\times 2$. Camera lucida drawings from cut sections and cellulose peels at intervals of 0.5 (a), 2.5 (b), 6.0 (c), 8.3 (d), 9.9 (e), 12.2 (f), 14.7 (g), 17.0 (h), and 20.0 mm. (i) below the top of the theca. Sections are not oriented according to convention as the position of the anus cannot be determined, but the radials (R) have been numbered clockwise from above. Deltoids (D) and infradeltoids (ID) are also indicated. Floor plates above the radials can be easily differentiated by the suture and the central canal (dark shaded), but in the upper part of the theca, floor plates fuse with deltoids and cannot be separated.

Similar canals are shown in a section of another fragmentary specimen, paratype USGD 2311 (text-fig. 3c). However, a somewhat different arrangement of canals can

be seen in the other sections of this specimen (text-figs. 3, 4). In one of these, the floor plates resting on radial R3 have two small tear-drop shaped canals instead of a larger central canal (text-figs. 3*a*, 4*a*). Two sutures which extend from the canals to the ambulacral groove seem to parallel cleavages in calcite of the floor plates; they separate the floor plates into inner and outer parts. In the other, the floor plates lying on the radial

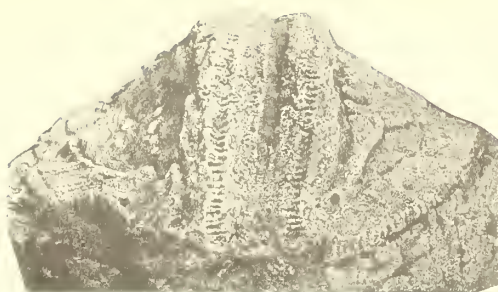


TEXT-FIG. 3. *Astrocystites distans* sp. nov. Slightly oblique cross sections of paratype, USGD 2311, $\times 2$. Camera lucida sketches of thin sections at intervals of 2 (*a*), 7 (*b*), and 12 mm. (*c*) below upper surface of specimen shown in Plate 100, fig. 5. Radials (R) are numbered, and deltoids (D) and infradeltoids (ID) are also indicated.

R4 have three small canals, two lateral and one medial which lies on the line of suture of floor plates just inside the ambulacral groove (text-fig. 3*b*, 4*b*). This medial canal appears to be connected with the laterals by sutures or narrow passages, which thus separate the inner and outer parts of the floor plates, as in the previous example; the inner superficially resembles the lancet plate of blastoids. This is directly underlain by what seems to be another thin plate, but on closer study under polarised light this proves to be a part of R4.

EXPLANATION OF PLATE 99

Figs. 1–10. *Astrocystites distans* sp. nov. 1, 2, Holotype, USGD 2302, $\times 3$, side and oral views showing straight, petaloid right postero-lateral ambulacrum with slit-like pores and ambulacral groove, and posterior interradius with crenulations and hydropore near the apex. 3, Holotype, USGD 2302, $\times 4$, detail of posterior interradius showing gentle to deep crenulations with vague, small tightly fused infradeltoids surrounding the anal opening and a small, circular hydropore near the apex. 4, Paratype A, USGD 2303, $\times 4$, showing straight ambulacrum and radials with gentle crenulations. 5, Paratype A, USGD 2303, $\times 8$, detail of a row of slit-like pores in the medial part of the ambulacrum. 6, Paratypes B–D, USGD 2309, $\times 3$, two longitudinal sections (paratype B, top left; paratype C, centre) and basal plate (paratype D, bottom right); B, section showing large vertical interrarial element; C, longitudinal section intersected nearer to the outer margin of the theca than in paratype B, and therefore only exhibiting traces of the interrarial element; D, fragmentary basal with small apical opening. 7, Paratype, USGD 2304, $\times 4$, oblique view of a single row of slit-like pores penetrating tightly fused floor plates with pores on either side and interrarial element at the apex. 9, Paratype, USGD 2313, $\times 4$, small, convex basal with radial crenulations and small apical opening. 10, Paratype, USGD 2314, $\times 4$, convex basal with strong radial, crenulations and small apical opening. Photographs by G. Z. Foldvary and B. D. Webby.



2



3



1



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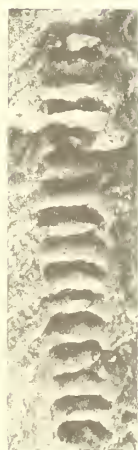
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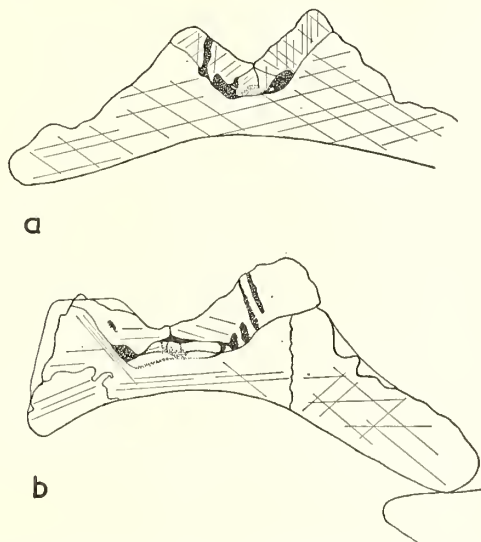


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4

Remarks. *Astrocystites ottawaensis* may be distinguished from *A. distans* by having pores with a circular cross-section, a wider spacing of pores (15 per cm.), and a slit-like hydropore. Few other features can be compared closely because only three specimens of the more perfectly preserved *A. ottawaensis* have previously been studied and details of internal structures are unknown. There are also differences of interpretation of certain structures which must be clarified before close comparisons can be made. For instance, Bather (1914*b*, pp. 196, 199) stated that the radials slope upwards towards the



TEXT-FIG. 4. Enlarged sections of parts of paratype, USGD 2311, $\times 7$. *a*, radial R3 consists of a large calcite crystal with prominent cleavages. It is overlain by floor plates also exhibiting cleavages. Each floor plate has a tear-drop shaped canal, the left also having a connecting pore. An area of recrystallized calcite (lightly stippled) lies between the canals. In addition to the vertical suture between floor plates, there are inclined sutures extending towards the ambulacral groove which seem to parallel cleavages in the calcite of the floor plates. *b*, radial R4 of text-fig. 3*b* consists of a large plate with two faint sutures (one irregular) of unknown significance, and prominent cleavages. Pores in the overlying floor plates seem to be connected to three small canals, two lateral and one medial. The medial canal lies on the suture between adjacent floor plates just below the ambulacral groove, and seems to be joined by sutures or passages to the lateral canals. They divide the floor plates into inner and outer parts. The lightly stippled area consists of recrystallized calcite.

ambulacral grooves from the top of the interradial sutures, and are notched for the excavation of the ambulacral grooves 'so that the pores between the floor-plates pass through into the thecal cavity'. Hudson (1925, 1927) and Fay (1962), on the other hand, considered that the radials slope downwards from the top of the interradial sutures rounding the distal ends of the ambulacral grooves.

Another edrioblastoid has recently been collected from the Trelawney Beds of northern New South Wales, which Philip (1966), on the basis of conodont work, regarded as Upper Caradocian (i.e., Trentonian–Maysvillian of North America). The edrioblastoid specimen (USGD 3304) consists of the upper part of an incomplete theca cut in longitudinal section, 1 cm. wide, and exhibiting fused deltoids and floor plates with slit-like

pores. It probably represents a species of *Astrocystites* comparable with *A. distans*, but until more material is found closer comparisons cannot be made.

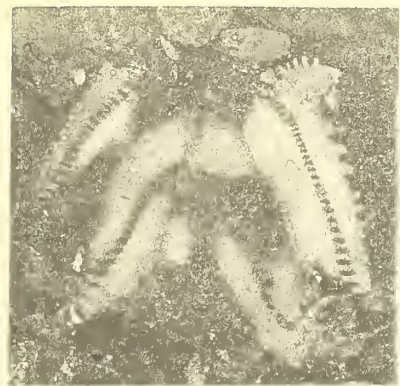
Discussion of edrioblastoid relationships. Bather (1914b, p. 202), while observing the similarities in the nature and arrangement of the floor and cover plates in *Astrocystites* and *Edrioaster*, noted that the ambulacra in *Astrocystites* are not sinuous, the cover plates in the oral region are arranged in a different manner, and the floor plates are more rigidly fused. The interradian element of *E. bigsbyi*, formed by the fusion of four floor plates (Bather 1914a, p. 165, text-fig. 3), is very different from that in *A. distans*, which is a large rod-like structure flanked by shorter, thin plates inclining towards the element because of the curvature of the theca. The pores in *Edrioaster* pass directly into the thecal cavity through the entire length of the ambulacra, whereas, at least in *A. distans*, they only pass directly into the thecal cavity in the proximal part of the ambulacra. Distally they lead into a canal which apparently opens into the thecal cavity at the top of the radial.

In *A. distans* the hydropore is centrally situated and near the apex of the posterior interradius. Leading from it the stone canal consists of an outer, centrally placed funnel-shaped chamber linked by a narrow oblique canal to an inner double chamber. This lies between the interradian element of the posterior interradius and the left posterior ambulacrum, and is connected to the interior of the theca by a short, narrow canal (text-fig. 5). This arrangement differs from that described by Kesling and Mintz (1966) in the edriasteroids *Isorophus cincinnatiensis* (Roemer) and *Carneyella pilea*

EXPLANATION OF PLATE 100

Figs. 1–8. *Astrocystites distans* sp. nov. 1, 2, Paratype, USGD 2310, $\times 3$, slightly oblique cross-sections at intervals of 2.5 and 17 mm. below the top of the theca; photographed from cellulose peels; 1, Section through two ambulacra showing thickened deltoids and solidly fused floor plates penetrated by pores, which gradually diminish in size proximally (see text-fig. 2b). 2, Section showing two ambulacra near their distal ends resting on radials; pores extend through floor plates into a canal overlying the radial; outer surface of radials show strong crenulations and interior surface is smooth (see text-fig. 2h). 3, Paratype, USGD 3303, $\times 3$, internal view of adoral part of posterior interradius showing nature of the stone canal and its relationship to the interradian element. 4, Paratype, USGD 2305, $\times 3$, longitudinal section showing thickened deltoids and fused floor plates penetrated by slit-like pores. 5, Paratype, USGD 2311, $\times 1.5$, side view of specimen before sectioning showing two ambulacra separated by an inter-ambulacral area; ambulacra rest on radials R1 and R5 respectively (see text-fig. 3). 6–8, USGD 2311, $\times 5$, thin sections at intervals of 2, 7, and 12 mm. below upper surface shown in fig. 5. 6, slightly oblique section across thecal plates showing surface crenulations and calcite cleavages in the plates; two ambulacra lie on radials R2 and R3 (for interpretations see text-figs. 3a, 4a). 7, section showing radials, R4 and part of R5, and overlying floor plates (see text-figs. 3b, 4b). 8, oblique section near distal ends of ambulacra showing them lying in grooves on radials R1 and R5 (see text-fig. 3c). Note prominent central canal in each ambulacrum below the floor plates, and well-developed cleavages in calcite of the radial plates.

Figs. 9–16. Miscellaneous pelmatozoan plates. 9, USGD 2307, $\times 3$, large thecal plate. 10, USGD 3300, $\times 3$, circular structure with stellate grooving, and another obliquely cut structure. 11, USGD 2315, $\times 3$, large round columnal with stellate axial canal. 12, USGD 3301, $\times 3$, round columnal with stellate axial canal and crenellae on part of the articulating surface. 13, USGD 3302, $\times 3$, small round columnal with round axial canal. 14, USGD 2307, $\times 3$, round columnal with round axial canal and concentrically grooved articulating surface. 15, USGD 2316, $\times 3$, part of stem showing alternate nodals and internodals. 16, USGD 2315, $\times 3$, small, round articulated columnals. Photographs by G. Z. Foldvary and B. D. Webby.



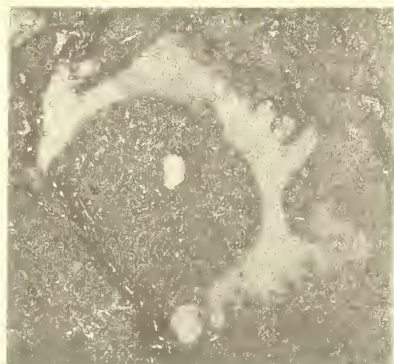
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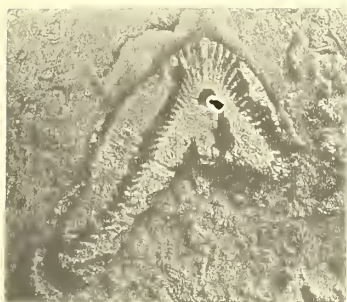
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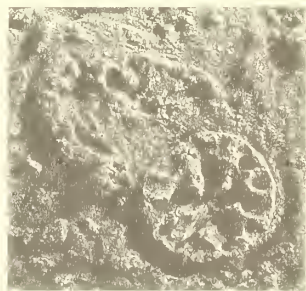
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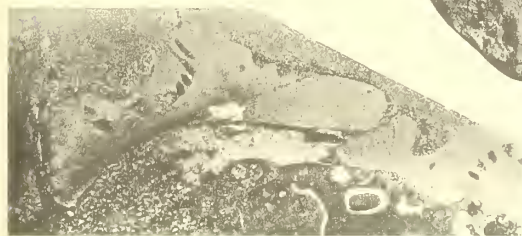
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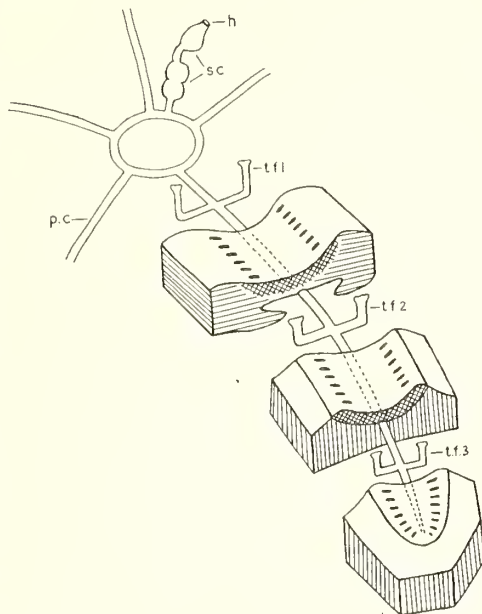


8

(Hall), where the stone canal extends from the hydropore inwards between the posterior interradius and the right posterior ambulacrum. A similar arrangement is exhibited by *Lepidodiscus fistulosus* (Anderson 1939). On the other hand, Bather (1914a, p. 168) observed that in *Edrioaster bigsbyi* the hydropore becomes deeper adorally and in the direction of the left posterior ambulacrum, suggesting a similar pattern to *A. distans*.

Bather (1915, p. 266) concluded that in edrioasteroids (including *Astrocystites*) the ambulacra exhibited an open system (similar to that in asteroids), viz., ampullae in the thecal cavity connected by way of the pores to tube feet and the perradial canal lying in the ambulacral groove. The tube feet were presumed to have acted both in respiration and feeding of the animal. Cover plates were evidently opened when *Edrioaster* was feeding. Anderson (1939, p. 75), in contrast, considered that in *Lepidodiscus fistulosus* and forms described by Bather, including *Astrocystites*, a closed system (as in echinoids) was represented, viz., a perradial canal below the ambulacral groove connected to external tube feet and internal ampullae. The evidence from the study of *A. distans* supports Anderson's suggestion for a closed ambulacral system, but the nature of the closed system differs. Whereas in *L. fistulosus* the theca is flexible and the ampullae and perradial canal lie internal to the skeleton, in *A. distans* the theca is rigidly fused and both ampullae and perradial canal are enclosed between radial and floor plates in the distal parts of the ambulacra, along the lines of the ophiuroid pattern (Nichols 1966, p. 109, fig. 15e), and internal to the skeleton in proximal parts of the ambulacra. In a section across the radial and floor plates in the distal part of one ambulacrum (see text-fig. 4b), side branches from the medial (perradial) canal lead through the floor plates to pores on the surface. Presumably the side branches contained enclosed ampullae which were surrounded by muscles capable of protraction, and were connected to tube feet occupying the pores.

In text-fig. 5 the inferred water vascular system in *A. distans* is represented. Judging from the nature of the pores, the tube feet in the proximal part of the ambulacrum were probably thinner and longer (text-fig. 5, t.f. 1) than those situated medially (t.f. 2), and



TEXT-FIG. 5. Schematic perspective diagram of part of one ambulacrum and the inferred water vascular system in *Astrocystites distans*. Deltoids are represented by horizontal lines, the radial by vertical lines and the floor plates by crossed lines. Cover plates are not shown. Hydropore (h) and stone canal (s.c.) are situated in the posterior interradius. The stone canal consists of funnel-shaped and double chambers linked by a narrow canal, and connected to a ring canal with a perradial canal (p.c.) leading into each ambulacrum. Three types of tube feet are suggested: long, slender forms (t.f. 1) which penetrate the thickened plates in the proximal region; shorter, thicker forms (t.f. 2) in the medial region; and shorter, thinner forms (t.f. 3) which protude through the rather thin floor plates lying on the radial in the distal region.

penetrated floor plates and possibly margins of deltoids as well. Distally, the tube feet appear to become thinner and shorter (t.f. 3). From the morphology of the inner, double chamber of the stone canal it may be tentatively suggested that it contained valves which regulated the flow of water through the system.

Specimen B of Bather's description of *A. ottawaensis* exhibited the most complete set of cover plates, the proximal and medial parts being covered but not the distal. Bather (1914b, p. 199) added that there was 'no reason to doubt that they were continuous . . . to the extreme end of the floor plates.' It seems probable that the cover plates opened along the margins of each ambulacrum, allowing the tube feet to protrude as in edrioasteroids. The cover plates in the oral region, however, are more irregular in size and shape, with smaller plates intercalated. There are, in addition, triangular oro-tegmina plates lying with their broader ends on interambulacral areas, and narrower ends reaching almost to the oral pole. It may be assumed from this arrangement that the circle of oro-tegmina and cover plates in the oral region was fixed, and the smaller pores underlying this region, as seen in *A. distans*, contained slender, elongated tube feet. The tube feet of this region may have been mainly sensory and respiratory in function, whereas those in medial and distal parts of the ambulacrum served also in feeding.

Edrioasteroids range from the Lower Cambrian to the Lower Carboniferous, evolving most rapidly in the Ordovician. From the close similarities in plating of the ambulacra and in the nature of the posterior interradius, there seems to be little doubt that during the Middle Ordovician the small, stalked group of edrioblastoids evolved from the basic edrioasteroid stock. Both *Astrocystites* and *Edrioaster* exhibit a hydropore and a cluster of plates around the anus in the posterior interradius. However, *Astrocystites* may be distinguished from *Edrioaster* by the pyriform shape of the theca, the rudimentary stem and, to a certain extent, by the stabilization of the number of thecal plates—five basals, five radials, and five deltoids.

Astrocystites superficially resembles blastoids like *Pentremites* but exhibits fundamental differences. No hydrospires, brachioles or spiracles can be recognized. Even if an internal soft-bodied chamber analogous to a hydrospire existed, it must have been restricted to the region below the proximal part of each ambulacrum, for the pores in the distal part communicate with a medial (perradial) canal lying between the radial and floor plates. If the pores had solely a respiratory function, some type of soft structures, like brachioles attached to floor plates and capable of extension on opening of cover plates, must have been present to catch and direct food particles towards the mouth. However, there is no direct evidence to support any of these speculations, and it must be concluded that edrioblastoids are morphologically distinct from blastoids.

Fay (1962, p. 205; 1967, pp. 242, 286) suggested that some form related to *Astrocystites* could have been ancestral to the blastoids which, according to him, appear in the Middle Silurian and range into the Permian. For an *Astrocystites*-like form to give rise to spiraculate blastoids the following changes would be required: (1) the development of a stem with definite columnals, (2) resorption of two sutures to produce three basals; (3) fusion of the infradeltoids with the deltoids; (4) reduction by fusion in the number of anal plates in the posterior interradius; (5) atrophy of the tube feet and infolding of the deltoids and radials to form the hydrospire; (6) replacement of a single hydropore at the upper extremity of the posterior interradius by a spiracle at the top

of each deltoid (some blastoids develop paired spiracles); (7) migration of radial canal inward or outward, and consequent secretion of calcium carbonate to form the lancet plate; and (8) development of brachioles. This, however, would entail more radical changes than by deriving blastoids, in the more generally accepted fashion, from cystoids through the transitional Middle Ordovician form *Blastoidocrinus* (Nichols 1966, pp. 146–8). Moore (1954) suggested derivation from a rhombiferan *Cystoblastus*-like ancestor by shifting of radials downward, laterals upward and partial fusion of basals. Brachioles were already developed, and hydrospires have been shown to be homologous with pore rhombs. However, the derivation of the lancets by modification of the radials seems too conjectural for the ready acceptance of this view.

Miscellaneous pelmatozoan plates. In addition to the thecal plates and fragments which can be positively recognized as parts of *A. distans*, there are numerous stem ossicles and a few plates from the Cliefden Caves locality which cannot be so confidently determined. Two main types of stem columnal can be distinguished; those with a stellate axial canal and those with a circular axial canal. The largest columnal (USGD 2315) is round, 5 mm. in diameter and has a stellate axial canal; part of the articulating surface shows faint crenellae, but it is otherwise smooth (Pl. 100, fig. 11). Another round columnal (USGD 3301), 3·8 mm. in diameter, also shows a stellate axial canal and a patchy development of crenellae on the articulating surface (Pl. 100, fig. 12). The columnal USGD 3302 is 2·0 mm. in diameter, has a small round axial canal and a smooth flat articulating surface (Pl. 100, fig. 13). Another (USGD 2307) is 2·3 mm. in diameter, has a larger round axial canal, and a concentric groove on the articulating surface (Pl. 100, fig. 14). In specimen USGD 2316 a pattern of round alternating nodal and internodal columnals is shown; the nodals have a diameter of 2·5 mm. and the internodals 2·0 mm.; the columnals are spaced about six in 4 mm. (Pl. 100, fig. 15). A thinner articulated specimen (USGD 2315) has round columnals, 1·2 mm. in diameter, and of uniform size, averaging five in 4 mm. (Pl. 100, fig. 16).

It is not possible at the present time to assign any of these columnals to *A. distans*. None of them seem to be comparable with the elements of the stem in *A. ottawaensis*. Bather (1914b) described the stem as circular and composed of pentameres, and Fay (1962) similarly observed that it was made up of curved polygonal plates grouped into three columnal rings each with five or more plates. Certainly the variety of stem columnals from the Cliefden Caves locality strongly suggests the presence of at least one other pelmatozoan in the fauna. This is confirmed by two other finds. The first is a large plate (USGD 2307) 14·5 mm. wide and 8 mm. high, with a radiating pattern of fine crenulations, three on the left side, six medial, and three on the right side; it is up to 3 mm. thick on the upper edge (Pl. 100, fig. 9). It resembles a cystoid thecal plate, and it is possible that a pore rhomb has been eroded from the thickened upper edge. Secondly, in USGD 3300, there is a circular structure with five grooves radiating from the centre (Pl. 100, fig. 10). The grooves subdivide away from the centre, and there seems to be a development of partitions across the grooves towards the periphery, forming facets possibly for the attachment of brachioles. To one side of the circular structure there appears to be a less well-defined, obliquely cut structure. The circular structure resembles the oral region of certain rhombiferan cystoids, for example, *Glaphyrocystis* Jaekel and *Echinoencrinites* Meyer (Hecker 1964, pl. 3, fig. 9b; text-fig. 19), or the eocrinoid

Cryptocrinus (Bather 1900, p. 70, text-fig. 37). It is possible that the isolated large plate and the circular structure belong to the same species. The only rhombiferan cystoid previously described from the Ordovician of Australia is *Cheirocrinus merrilleesi* Brown 1964, which has very different ornamentation on thecal plates.

Eocrinoids have not yet been reported from Australia.

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B. D. WEBBY

Department of Geology and Geophysics

University of Sydney

Sydney, N.S.W.

Australia

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CHUBBINA, A NEW CRETACEOUS ALVEOLINID GENUS FROM JAMAICA AND MEXICO

by E. ROBINSON

ABSTRACT. *Chubbina jamaicensis* gen. et. sp. nov. and *Chubbina macgillavryi* sp. nov. from the Cretaceous rocks of Jamaica and southern Mexico are described. *Borelis cardenasensis* Barker and Grimsdale is placed in the new genus. *Chubbina* appears to be a useful index for the Upper Cretaceous (Upper Campanian to Maastrichtian) of the Greater Antilles and Central America.

IN 1937 Barker and Grimsdale described a new alveolinid species, *Borelis cardenasensis*, from the Cardenas beds of north-eastern Mexico. In this description they doubtfully referred the species to *Borelis*, mainly on the grounds that it bore a superficial resemblance to *Borelis jamaicensis* Vaughan and *Borelis matleyi* Vaughan (1929). Cole (1956) showed that both of Vaughan's species belonged to the genus *Fabularia*.

Under *Cosinella*, Reichel (1937, p. 136 n.) mentioned a manuscript species of Schlumberger and compared it with *B. cardenasensis* but no description of *Cosinella* was given either then or subsequently. Reichel has indicated (pers. comm., 1966) that he is still in possession of Schlumberger's manuscript material for *Cosinella*, which must remain a nomen nudum. Nevertheless the name *Cosinella* was used, without further description, by Dunnington *et al.* (1960, p. 61) for specimens subsequently described by Smout as *Pseudedomia globularis* (1963), and was also considered by Seiglie and Ayala (1963) for specimens resembling *B. cardenasensis* found in the Cuban Maastrichtian. Smout (1963, p. 225) in emending the genus *Pseudedomia*, briefly discussed *B. cardenasensis*, suggesting, on the basis of information received from Grimsdale, that the species had a uniserial termination and was, therefore, possibly related to *Raadshoovenia* van den Bold (1946). On the other hand Colalongo (1963) included *B. cardenasensis* in her new genus *Sellialveolina*, apparently on the basis of the original description.

During studies of the Cretaceous inliers of Jamaica, undertaken by the Geology Department of the University of the West Indies, numbers of larger foraminifera have been collected, amongst which are numerous examples of an alveolinid related to '*Borelis*' *cardenasensis*. The internal structures of the Jamaican form are also similar to those of *Pseudedomia* and *Sellialveolina*, although the mode of coiling is basically different.

On the basis of an examination of the Jamaican material, which contains a large number of microspheric individuals, the new genus *Chubbina* is proposed, with *Chubbina jamaicensis* sp. nov. as the type. '*Borelis*' *cardenasensis* is considered to be congeneric with the Jamaican form. Recently Professor H. J. MacGillavry kindly sent me thin sections of a complanate alveolinid which he collected in southern Mexico. These specimens also belong to *Chubbina* and are further described below.

Acknowledgements. I wish to thank Dr. A. H. Smout for reading part of the manuscript of this paper and Mr. R. DeSouza who assisted with the photography. The new genus is named for Dr. L. J. Chubb, in appreciation of his work on the Cretaceous of the Caribbean area.

Location. The species described have come from the following localities.

Locality 1. ER 108, on the railway between Catadupa and Cambridge, Jamaica, W.I., at the tenth telegraph pole, plus 20 ft., after milepost 96.

Locality 2. ER 213A, three-quarters of a mile west of Frankfield, Parish of Clarendon, Jamaica, W.I., at Guinea Corn, in the bed of the Rio Minho, in the type section of the Guinea Corn Formation (Coates 1965), about 40 ft. stratigraphically below the top of the limestone.

Locality 3. Type locality for *Chubbina cardenasensis* (Barker and Grimsdale 1937).

Locality 4. On the road between Tuxtla Gutierrez and Ocozucua, state of Chiapas, Mexico, at stop 2, K.1061, (fig. 1, Excursion C-15-b, 20th International Geological Congress, Mexico, 1956).

Figured specimens are deposited at the British Museum (Natural History) (BMNH).

SYSTEMATIC DESCRIPTIONS

Family ALVEOLINIDAE Ehrenberg, 1839

CHUBBINA gen. nov.

Type species, Chubbina jamaicensis sp. nov.

Diagnosis. Test with walls composed of microcrystalline calcite, imperforate, probably originally porcellaneous; in the megalospheric generation subglobular or lenticular, becoming discoidal in the mature microspheric form; chamber coiling markedly streptospiral in the early stages, becoming almost planispiral in the last whorls of the microspheric generation; involute, often becoming pseudevoluate in the later whorls and strongly recurved but not cyclical; the number of chambers per whorl increasing with the addition of each whorl and always being greater than two in the ephebic stage.

Dimorphism pronounced; the single, spherical proloculus of the megalospheric generation followed by a single tubular chamber, without internal structures; microspheric generation with a milioline nepiont; succeeding chambers subdivided into spirally directed, tubular chamberlets, embedded in a solid microcrystalline endoskeleton or 'couche basale'; chamberlets multiple, initially arranged in one or more tiers or layers, later becoming irregular in layering, with varying differentiation into a subepidermal layer of primary chamberlets and multiple supplementary chamberlets in the 'couche basale'; pre-septal canals present, irregularly equipped with buttresses; communication between chamberlets in successive chambers effected by means of rounded multiple apertures, more or less in alignment with the chamberlets.

Chubbina jamaicensis sp. nov.

Plate 101, figs. 1-6; Plate 102, figs. 1-5

Microspheric Form. Test free, subglobular to subdiscoidal, consisting of 6 to 8 streptospirally coiled whorls after the nepionic stage; early stages involute, forming a subspherical, immature test; at about the fifth whorl becoming flaring, with the development of a peripheral flange with an acute sub-angular margin; in the final whorl pseudevoluate and flaring, with a broad, complanate flange partly surrounding an excentric, umbonate region containing the earlier part of the coil; peripheral margin of the final whorl usually acquiring a stoutly rounded rim which may become equal in thickness to the umbonate region of the test; the distal, recurved face of the final whorl flattened, with sub-angular

margins, and provided with numerous round apertures, scattered more or less uniformly over the whole face.

Coil subdivided into chambers by septa which are the turned-in continuations of the spiral wall; chambers about 6 in number in the fourth whorl, rising to 15 in the final, complanate whorl; septa becoming increasingly recurved in the later whorls; alar prolongations of the chambers of the final whorl slightly vorticiform.

The microspheric nepiont was not clearly seen but appears to be milioline. The succeeding chambers are filled with a solid mass of microcrystalline calcite forming the 'couche basale', pierced by spirally directed, tubular chamberlets. The chamberlets are continuous between the distal and proximal septal walls of each chamber and the chamberlets of any one chamber are connected with the chamberlets of the preceding and succeeding chambers by more or less directly aligned rounded apertures in the septa. In each chamber the material of the 'couche basale' does not extend as far as the distal septum, but leaves a space, a pre-septal canal, allowing free communication between the chamberlets. However, the pre-septal canal is traversed irregularly by projections from the 'couch basale', which reach the distal septum forming buttresses.

The 3 or 4 chamberlets in the chambers of the first whorl are arranged in a single, more or less regular tier. In the second or third whorl the increasing number of chamberlets gives rise to a second tier below the first. At about the fourth whorl a third tier of chamberlets is gradually inserted. In the last-formed whorl the number of tiers or rows rises from 4 or 5 to 80 or 90. Subdivision of the chamberlets occurs in the region of each pre-septal canal, by the addition of apertures through the distal septum, from which additional chamberlets project into the next-formed chamber. The addition of chamberlets is a more or less continuous process, so that the second tier of chamberlets is acquired gradually and only becomes clearly defined over the space of 2 or 3 chambers. The later addition of tiers occurs in a similar manner and these are largely acquired through the multiplication of chamberlets, along the inner margin of the whorl. Although all the chamberlets are spirally directed, a degree of undulation or meandering occurs so that, beyond about the fourth whorl, they are no longer arranged in regular tiers but occur scattered uniformly in the 'couche basale'. The distance between adjacent chamberlets is approximately the same as the diameter of the chamberlets themselves in the final whorl. In the early whorls it is less. The chamberlets nearest to the spiral wall tend to be aligned more regularly along the wall.

EXPLANATION OF PLATE 101

Fig. 1. *Chubbina jamaicensis* gen. et sp. nov., cotype, microspheric form, sectioned normal to the axis of coiling of the final whorl, $\times 20$. BMNH P. 48049.

Fig. 2. *Chubbina jamaicensis* gen. et sp. nov., cotype, microspheric form, sectioned parallel to the axis of coiling of the final whorl, $\times 30$. BMNH P. 48048.

Fig. 3. *Chubbina jamaicensis* gen. et sp. nov., cotype, megalospheric form, sectioned to show the progressive change in direction of coiling in successive whorls, 'canal flexostyle' and buttresses. $\times 45$. BMNH P. 48052.

Fig. 4. Section through portion of terminal flange of *C. jamaicensis*, showing some differentiation of a subepidermal layer of chamberlets as seen in *Pseudodomia globularis* Smout. $\times 20$. BMNH P. 48050.

Fig. 5. Natural internal mould of a portion of several chambers from a microspheric individual of *C. jamaicensis*, showing tubular chamberlets and preseptal canals. $\times 16$. BMNH P. 48055.

Fig. 6. *Chubbina jamaicensis* gen. et sp. nov., cotype, external view, $\times 18$. BMNH P. 48056.

All specimens from Locality 1, Jamaica.



ROBINSON, *Chubbina* gen. nov.

Megalospheric form. Test much smaller than in the microspheric form, sub-globular to inflated lenticular, consisting of 4 to 6 streptospirally coiled, involute whorls, the last-formed whorl frequently showing a tendency to acquire a flaring end stage; megalospheric specimens with a fully complanate, pseudevoluate final stage not observed.

Internally there is a single, spherical proloculus, followed by a single, tubular chamber without internal structure, a 'canal flexostyle'. Further internal development closely parallels that of the microspheric form, but megalospheric specimens with more than 10 rows of chamberlets in the last whorl, when seen in spiral section, have not been observed.

Critical measurements of *C. jamaicensis* are included in Table 1. Text-fig. 1 shows the size range of specimens of *Chubbina* from Jamaica and elsewhere.

Type locality. Locality 1. Additional material from locality 2.

Chubbina cardenasensis (Barker and Grimsdale 1937)

1937 *Borelis cardeuasensis* Barker and Grimsdale, p. 173, pl. 9, figs. 1-5.

Examination of Barker and Grimsdale's original figures and of additional syntypes reveals that pre-septal canals or passages are present, and occupy the space in each chamber in front of the incomplete transverse septa mentioned by Barker and Grimsdale. No true buttresses are visible on any of the original figures, but one can see that buttresses are probably present from an examination of figures 3 and 4 of the original description. These show a certain irregularity in the shape of the spiral and transverse septa of Barker and Grimsdale, where parts of the sections are cut through the pre-septal canals. Dr. C. G. Adams of the British Museum (Natural History) has confirmed that no specimens likely to represent a microspheric form are present amongst Grimsdale's syntypes.

Chubbina cardenasensis differs from *C. jamaicensis* primarily in the rate of chamber enlargement. This is more rapid in *C. jamaicensis* resulting in the insertion of the third tier of chamberlets in the third or fourth whorl. In *C. cardenasensis* the third tier of chamberlets is not inserted until the fifth whorl or later.

Chubbina macgillavryi sp. nov.

Plate 102, figs 8; Plate 103, figs. 3, 4; see also Plate 102, figs. 6, 7

Thin-sections of a limestone collected in southern Mexico by Professor H. C. MacGillavry and sent to the author, contained numerous random sections of *Chubbina*. They differ from *C. jamaicensis* and *C. cardenasensis*. The coiling is streptospiral, but the degree of eccentricity of the coiling is more variable than in the other two species. Some specimens, typified by that illustrated on Plate 103, fig. 3, are similar in their coiling mode to *C. jamaicensis*. Other specimens may approach a planispiral mode (Pl. 102, fig. 6). *C. macgillavryi* resembles *C. cardenasensis* in the relatively low rate of chamber enlargement. The third tier of chamberlets is normally inserted at about the fifth whorl. In some specimens even the second tier is not inserted until the fourth or fifth whorl. The preseptal canals of *C. macgillavryi* are narrower than in either *C. jamaicensis* or *C. cardenasensis* and the proloculus of the magalospheric generation is also larger. Table 1 compares some of the critical measurements. A single, uncentred

section of a microspheric individual (Pl. 103, fig. 4) is larger than the largest example of *C. jamaicensis* yet found. All the available thin sections show that the chamberlets of the first few chambers are relatively rectangular in cross-section with thin walls.

Type locality. Locality 4.

TABLE 1.

Comparison of some critical measurements of species of *Chubbina*.
(A) *C. jamaicensis*, (B) *C. cardenasensis*, (C) *C. macgillavryi*.

	A	B	C
	μ	μ	μ
Diameter of chamberlets	40–55	60	25–50
Spacing between chamberlets	30	10–30	10–20
Distance across pre-septal canal	90–140	120	25–100
Diameter of proloculus	100–180*	90–120	150–300†

* Only one specimen of *C. jamaicensis* has a proloculus reaching 180 μ in diameter. The next largest measured was 140 μ .

† Although all the magalospheric specimens of *C. macgillavryi* had large proloculi, there was some degree of recrystallisation at the centres of many individuals, making accurate measurement difficult.

Discussion. The specimens illustrated by Seiglie and Ayala-Castanares (1963, pl. 1, figs. 2 and 3 appear to belong to *Chubbina cardenasensis*. The section illustrated by these authors as *Rhapidionina* sp. (ibid., p. 27; pl. 1, fig. 1) is rather indistinct, but could be a portion of the terminal flange of *Chubbina*.

Most of the skeletal features mentioned in the preceding descriptions have already been noted in discussions of the complanate genus *Pseudedomia* by Eames and Smout (1955), Smout (1963) and Reiss *et al.* (1964). The major difference between *Pseudedomia* and *Chubbina* lies in the streptospiral mode of coiling in the latter genus. This coiling eccentricity continues on a diminishing scale throughout ontogeny and is readily distinguishable from the slight irregularities which may develop in a large specimen of *Pseudedomia*, due for instance to environmental conditions. The eccentricity is apparent in most thin sections of *Chubbina* but it is only when a centred thin section happens to be cut normal to the axis about which the coiling plane rotates that the degree of rotation can be measured (Pl. 101, fig. 3).

EXPLANATION OF PLATE 102

Figs. 1, 2, and 4. *Chubbina jamaicensis* gen. et sp. nov., cotypes, all megalospheric individuals from Locality 1, showing limits of variation in rate of chamber enlargement and a progressive deterioration in the state of preservation of successive chamber walls, possibly due to diagenetic effects.

Fig. 1, BMNH P. 48051, fig. 2, BMNH P. 48053, fig. 4, BMNH P. 48047.

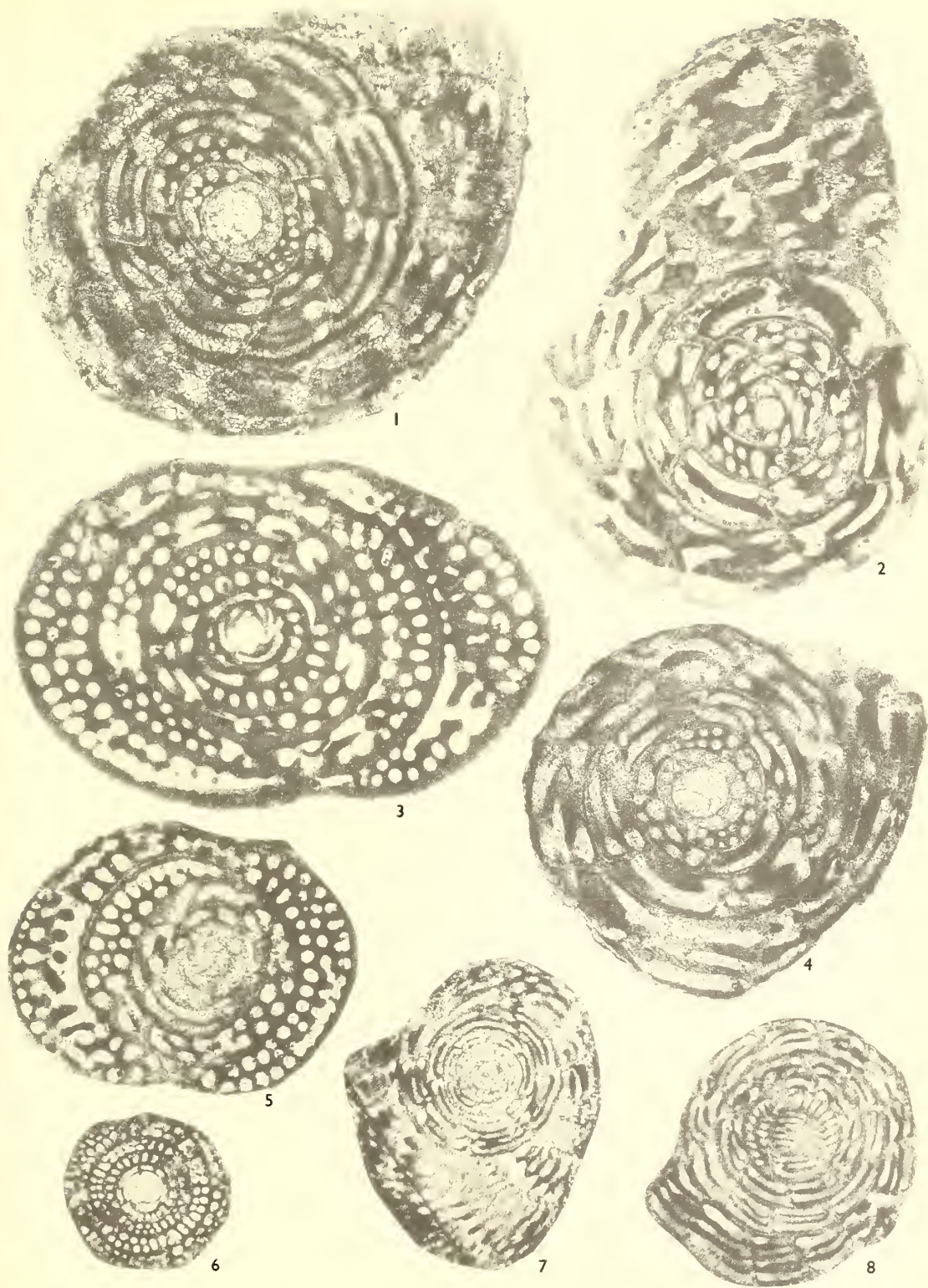
Fig. 3. *Chubbina jamaicensis*, megalospheric form, from Locality 2. $\times 45$. BMNH P. 48054.

Fig. 5. Off-centred section of *C. jamaicensis* from Locality 1, showing preseptal canals, buttresses and some differentiation of a subepidermal layer of chamberlets in the last whorl. $\times 45$. BMNH P. 48046.

Fig. 6. *Chubbina* sp. cf. *C. macgillavryi* sp. nov., Locality 4, showing canal flexostyle, relatively low rate of chamber enlargement and relatively thin walls between chamberlets. $\times 30$. BMNH P. 48042.

Fig. 7. *Chubbina* sp. cf. *C. macgillavryi* sp. nov., Locality 4. ? microspheric individual. $\times 30$. BMNH P. 48040.

Fig. 8. *Chubbina macgillavryi* sp. nov., cotype, Locality 4. Off-centred section of megalospheric specimen. $\times 30$. BMNH P. 48041.



The partitioning of the chambers, with the resultant chamberlets, preseptal canals, and buttresses, is very similar to that of *Pseudedomia globularis* Smout. Unlike those seen in *P. drorimensis* Reiss *et al.*, the chamberlets resemble tubes excavated in a solid 'couche basale' rather than chamberlets enclosed by regular, spirally directed partitions. The irregularity in chamberlet formation in the later chambers suggests that chamber division is not ordered by the secretion of subepidermal partitions, but occurs through the somewhat random development of spirally directed tubular filaments which surround themselves with a solid skeletal framework. The loss of regular tiering in the later stages is due to the confining influence of the spiral wall, which becomes progressively both higher and relatively narrower, forcing the tubular filaments to accommodate themselves within the available space. It is for this reason that the distinction between primary and secondary chamberlets, noted by Smout, for instance in the case of *P. globularis* (1963), is not here considered important. The distinction is sometimes seen in specimens of *Chubbina* (Pl. 101, fig. 4) but the development of primary chamberlets is irregular. The outermost chamberlets in any one chamber are confined in their position by the enclosing spiral wall, which is secreted first, by a process separate from that producing the 'couche basale'.

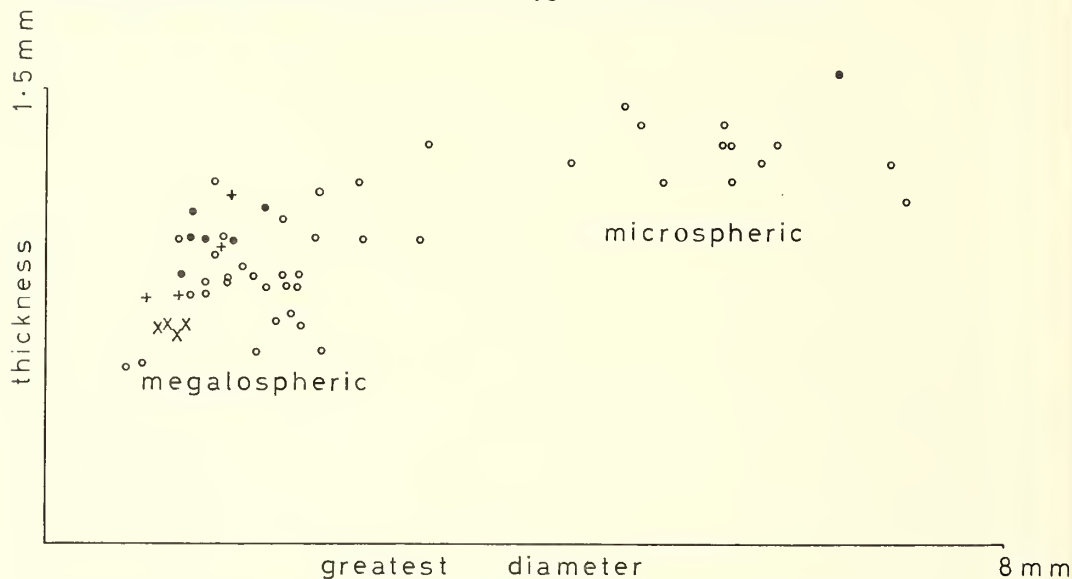
Chubbina resembles *Selliaveolina vialli* Colalongo in its gross internal structure and it is possible that *S. vialli* possesses a yet undiscovered complanate end stage. However the diagnosis for *Selliaveolina* should be emended to exclude *Chubbina cardenasensis*. Colalongo specifically mentions (1963, p. 7) as one of her distinctions between *S. vialli*, the genus type, and '*Borelis*' *cardenasensis*, that in '*B.* *cardenasensis*': 'the coiling of the first whorls is streptospiral but in *S. vialli* it is always planispiral' (trans.). This distinction is considered here to be of generic importance, particularly as the stratigraphical and geographical distributions of the two forms are markedly different. On the other hand there is some justification for erecting a new subfamily to include complanate species of alveolinid.

Fourcade (1966) described the new genus *Murciella* from the Upper Cretaceous of Spain. The internal structures show that this form belongs correctly to the *Pseudedomia/Chubbina* group, and in my view, should also be included in the Alveolinidae, but the uniserial termination of its coil allows separation at the generic level. At the same time it should be noted that rare, megalospheric individuals in populations of *Chubbina jamaicensis* also terminate their growth with one or two uncoiled chambers. The apparently earlier appearance of *Murciella* in Europe (Bignot 1967) would preclude any direct connection with *Chubbina*.

Reiss *et al.* (1964) suggested that *Pseudedomia* could be related to the peneroplids through the development of excessive thickening of the subepidermal partitions to produce a 'couche basale'. It seems that a 'couche basale', with associated multiple rows of chamberlets, is developed characteristically in only two groups, the Alveolinidae (including complanate forms) and the so-called Fabulariinae, and this may suggest a close relationship. However, both groups evolve their multiple rows of chamberlets in different geological eras. Moreover, the Tertiary genus *Fabularia* retains a biloculine type of coiling, so that direct descent from a multiloculine Cretaceous alveolinid ancestor, with multiple rows of chamberlets, is unlikely. In Jamaica, *Fabularia* is seen to evolve from a primitive form with a single row of chamberlets (*Fabularia matleyi* (Vaughan)) through intermediate forms, retaining the single row of

chamberlets, but with basal thickening (*Fabularia vaughani* Cole), to advanced forms with multiple rows of chamberlets in a 'couche basale' (*Fabularia verseyi* Cole).

Another American species which appears to belong to the complanate alveolinid group is *Borelis gunteri* Cole. The type figures (Cole 1941, pls. 2, 18) are rather indistinct, but *B. gunteri* appears to be a planispiral form, like *Pseudedomia*. It may also be related to *Raadshoovenia* van den Bold, but both types need re-examination.



TEXT-FIG. 1. Measurements of thicknesses and greatest diameters of *Chubbina*.

Dots are *C. jamaicensis*, Locality 1.

Circles are *C. jamaicensis*, Locality 2.

× signs are syntypes of *C. cardenasensis* (Barker and Grimsdale), Locality 3.

+ signs are *C. macgillavryi*, Locality 4.

Distribution. *Chubbina* has been recorded from Mexico (Barker and Grimsdale, op. cit. and this paper), Cuba (Seiglie and Ayala, op. cit.) and Jamaica. There are a number of other records of Cretaceous alveolinids in the Caribbean and Central American region, which, on further investigation, would probably prove to be species of *Chubbina* (e.g. Bronnimann in Dixon 1956, p. 81, as *Cosinella*, from the upper Cretaceous of British

EXPLANATION OF PLATE 103

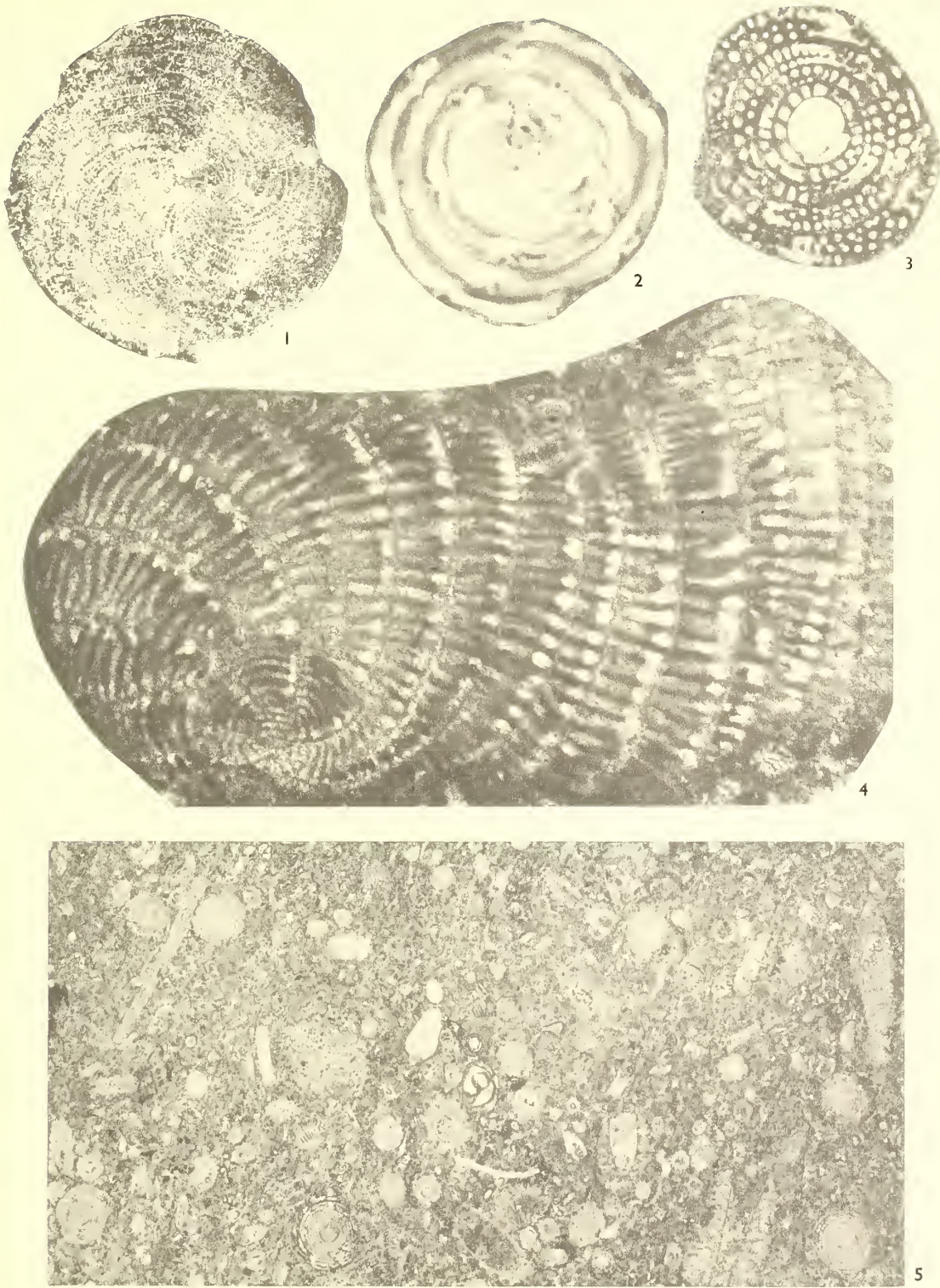
Fig. 1. *Ayalaina rutteni* (Palmer), from the lower part of the Guinea Corn Formation, near Locality 1, Jamaica. ×12. BMNH P. 48058.

Fig. 2. Undetermined alveolinid from Locality 4, having only a single layer of chamberlets in each chamber. ×30. BMNH P. 48039.

Fig. 3. *Chubbina macgillavryi* sp. nov., megalospheric cotype from Locality 4, showing large proloculus, canal flexostyle and low rate of chamber enlargement. ×30. BMNH P. 48043.

Fig. 4. *Chubbina macgillavryi* sp. nov. microspheric form, from Locality 4, section cut tangentially, normal to the axis of coiling of the final whorl. ×20. BMNH P. 48045.

Fig. 5. Part of a thin section from Locality 4, showing abundant specimens of *Chubbina*, rudistid fragments and an off-centred transverse section of *Ayalaina rutteni* (Palmer). ×8. BMNH P. 48044.



ROBINSON, *Chubbina* and *Ayalaina*

Honduras). Brown and Bronnimann (1957, p. 35). reported alveolinids from the type locality of *Kathina jamaicensis* (Cushman and Jarvis). This locality is only 20 metres from the type locality of *Chubbina jamaicensis* (which also contains *K. jamaicensis*).

In Jamaica *C. jamaicensis* is an index fossil for the group of limestones, including the Guinea Corn Formation of Coates (1965), which contains the *Titanosarcolites* rudistid fauna of Chubb (1955, pp. 178, 183) considered by him to be of Maastrichtian age. It is normally associated with *K. jamaicensis*, miliolids, and ostracodes. *Vaughanina cubensis minor* Seiglie and Ayala and *Sulcoperculina dickersoni* (Palmer) are also found at this horizon. Recently *Ayalaina rutteni* (Palmer) has been found for the first time in the same limestone group (Pl. 103, fig. 1, specimen donated by Mr. A. D'Aguilar of the University of the West Indies). Previously this species (as ?*Meandropsina rutteni*) had been recorded in Jamaica only from the limestones containing the *Barrettia* rudistid fauna, considered by Chubb to be of Campanian age (in Zans *et al.* 1962, pp. 11–15).

In the material from locality 4, *C. macgillavryi* occurs with *K. jamaicensis*, *Sulcoperculina* sp. and *Ayalaina* sp. In Cuba Seiglie and Ayala (op. cit.) consider the range of their '*Borelis*' cf '*B. cardenasensis*' (*C. cardenasensis* of this paper) as being upper Campanian to lower Maestrichtian. The types of *C. cardenasensis* come from a section which Barker and Grimsdale considered to be of Campanian to Maastrichtian age (op. cit.).

Chubbina, then, appears to be of regional stratigraphical value in indicating a late Campanian to Maastrichtian age for rocks in which it is found. In Jamaica the genus is also restricted to rocks whose general appearance and faunas indicate a shallow shelf or lagoonal environment (Coates 1965).

Although *Chubbina* may be the most common late Cretaceous alveolinid in the Americas, other genera do occur. One of these is a planispirally coiled form, apparently with only one row of chamberlets to each chamber. A single section of this form, collected from Locality 4, is illustrated on Plate 103, fig. 2.

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E. ROBINSON
Department of Geology
University of the West Indies
Mona
Jamaica

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FAMENNIAN AMMONOIDS FROM NEW SOUTH WALES

by T. B. H. JENKINS

ABSTRACT. Seven species and two subspecies belonging to four genera of ammonoids (Clymeniina and Goniatina) are described from a Famennian horizon, *Platyclymenia* Zone, a few hundred feet below the erosive base of the Carboniferous in the vicinity of Keepit Dam, near Tamworth, New South Wales. Three new species of Clymeniina are described: *Gemuclymenia keepitensis*, *Platyclymenia* (*Platyclymenia*) *teichertii*, and *P. (P.) alterna*.

ONLY in recent years have ammonoid cephalopods been reported in the Upper Devonian strata of eastern Australia. As Teichert remarked in 1948, the earlier records of ammonoids from those strata are probably erroneous. The first acceptable record of such fossils is that of Pickett (1960) who described a new species of clymenid from the Borah Limestone in northern New South Wales. Lately the index goniatite *Cheiloceras* has been recorded by the present writer and reference has been made to the fauna now described, both occurrences being in the same northern New South Wales province.

The stratigraphic horizons of these ammonoids have been previously indicated in a column for the area near Keepit Dam (Jenkins 1966, text-fig. 2), the horizon of the fossils now described being about 3,000 ft. higher, in an expanded, largely clastic succession, than that of the *Cheiloceras* occurrence. The persistent Borah Limestone seems to be absent in the belt of country running meridionally through Keepit Dam which has yielded the later ammonoid finds; its absence there is presumably due to the disconformity between the Devonian and Carboniferous systems. The inferred position of the Borah Limestone is thus an unmeasured distance, possibly as much as a thousand feet, above that of the fauna now described. The general geology of the surrounding country has been described by Voisey and Williams (1964).

All the fossils here described come from a 25 ft. lens of clayey coarse sandstone, containing patches of shale breccia, in the basal portion of the Mandowa Mudstone outcropping in Spring Gully at a point 3.13 miles N. 24° W. of Keepit Dam and 1.0 miles W. 27° S. of Gartmore Homestead. It is 1.5 miles N. of the *Cheiloceras* spot shown in text-fig. 1 of Jenkins (1966), the scale of which locality map should be corrected to 1 in. = 0.7 mile.

Recent discoveries of Late Devonian ammonoids in northern New South Wales provide a few firm correlations with other areas but the sequence of faunas is as yet only very imperfectly known in eastern Australia, in marked contrast to the position in western Australia, where ammonoids are now known from each of the major divisions, *Manticoceras*-Stufe to *Wocklumeria*-Stufe (Glenister and Klapper 1966).

Described specimens are in the fossil collections of The University of Sydney Geological Department and are referred to by USGD catalogue numbers.

SYSTEMATIC DESCRIPTIONS

Suborder CLYMENIINA Hyatt 1884

Superfamily CLYMENIACEAE Edwards 1849

Family CYRTOCLYMENIIDAE Hyatt 1884

Genus GENUCLYMENIA Wedekind 1908

Type species. Clymenia frechi Wedekind 1908, p. 617, by subsequent designation of Schindewolf 1957.

In its sutural character this genus is intermediate between the two other genera, *Cyrtoclymenia* and *Cymaclymenia*, included in the Cyrtoclymeniidae by Schindewolf, (in Moore, 1957). *Genuclymenia* is previously recorded from Germany and the Urals (U.S.S.R.).

Genuclymenia keepitensis sp. nov.

Plate 104, figs. 1-4; text-fig. 1 g, h

Derivation of name. From Keepit Dam, near Gunnedah, N.S.W.

Holotype. USGD 6827.

Preservation. The holotype is an internal mould in clayey sandstone; three other specimens are similarly preserved.

Dimensions (in mm.)

	D	WW	WH	UW
Holotype USGD 6827	16.8	c. 4.5	6.8	c. 5.5
USGD 6830	16.3	4+	6.9	5.7

Diagnosis. *Genuclymenia* with lateral lobe separated from umbilical seam by short straight radial segment of suture, flatly rounded whorl sides converging from maximum width near mid-flanks to a narrowly rounded venter.

Description. Shell form is subdiscoidal and rather narrowly umbilicate with whorls deeply overlapping; in cross-section the whorls are compressed with flatly rounded sides having maximum width at about mid-height and converging gradually to a narrowly rounded venter. Low ribs on part of one mould and faint growth-lines on its counterpart seem to mark a shallow lateral sinus passing into a broad ventro-lateral salient.

The external suture line runs radially from the umbilical seam and passes abruptly into a semicircular lateral lobe which is separated from the flat ventral saddle by a shallow lobe. The internal suture has not been observed.

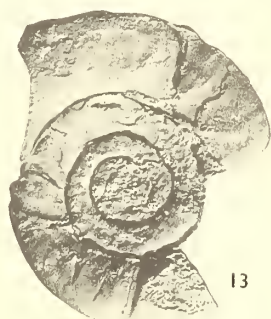
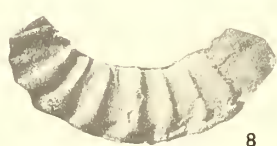
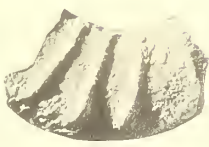
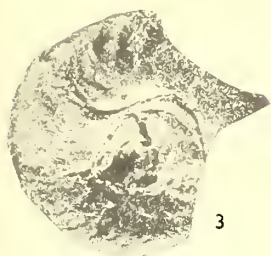
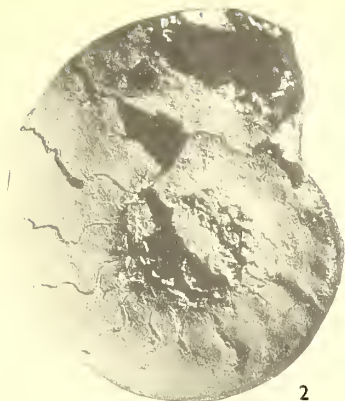
EXPLANATION OF PLATE 104

Figs. 1-4. *Genuclymenia keepitensis* sp. nov. 1, internal mould, USGD 6829, $\times 4$; 2, internal mould, holotype, USGD 6827, $\times 3$; 3, a partial internal mould, uncoated, showing suture and low ribs, USGD 6830, $\times 2$; 4, plasticine mould from counterpart of USGD 6830, showing low growth ridges, $\times 2$.

Figs. 5, 6. *P. (Platyclymenia) annulata annulata* (Münster). 5, internal mould, USGD 6834, $\times 1$; 6, fragment of an internal mould, USGD 6836, $\times 2$.

Figs. 7, 8. *P. (Platyclymenia) annulata densicosta* Frech. 7, internal mould, USGD 6837, $\times 2$; 8, external mould, USGD 6880, $\times 2$.

Figs. 9-13. *P. (Platyclymenia) teichertii* sp. nov. 9, crushed specimen preserving fine growth-lines, syntype, USGD 6839, $\times 1$; 10, internal mould, (subsequently sectioned for text-fig. 2e, f), syntype, USGD 6891, $\times 2$; 11, internal mould (see also text-fig. 2a-d), syntype, USGD 6890, $\times 2$; 12, internal mould showing septal face of body chamber, USGD 6851, $\times 1\frac{1}{2}$; 13, partly crushed internal mould showing portions of three septal faces, USGD 6850, $\times 1\frac{1}{2}$.





Remarks. Previously figured sutures of species assigned to *Genuclymenia* (see text-fig. 1) show an umbilical saddle passing immediately into a rounded lateral lobe. In *G. keepitensis* the lateral lobe is separated from the umbilical seam by a nearly straight radial portion of the suture which could be considered a flat saddle. Wide separation of lateral lobe and umbilical seam characterizes the related *Cynaclymenia* which has a broad saddle in this position. In the character of its dorso-lateral suture, the new species is thus intermediate between *Cynaclymenia* and other species of *Genuclymenia*. Of figured specimens it is closest to *Cynaclymenia pseudogoniatites* (Sandberger 1853, pl. 7, fig. 4 (others excluded)) which shows a slightly asymmetrical and incipiently acuminate lateral lobe (text-fig. 1i herein).

In shell form *G. keepitensis* is distinguished from Wedekind's species *G. frechi* and *G. discoidalis* by the absence of any flattening along its venter and from *G. angelini* by its more compressed whorls. *G. karpinskii* Perna has wider whorls ($WW/WH = 0.81$ at $D = 25$ mm.) and straighter lateral growth-lines meeting the umbilical seam more orthogonally than in *keepitensis*. *G. borni* Schindewolf is closest in shell shape but has maximum whorl width near the umbilical shoulder and lacks even the low ribs seen in some of the Keepit specimens.

Occurrence. According to Schindewolf (in Moore 1957) *Genuclymenia* is confined to the *Platyclymenia* zone of the Famennian, i.e. to Stufen III and IV of Wedekind (1913). *G. frechi* was recorded at Enkeberge by Wedekind (1908, table after p. 634) from beds that were later termed Stufen IV and V. But these tabulated records do not appear in the text, were not repeated by Wedekind (1914) and were not confirmed by Lange's (1929, p. 12 n., p. 88) later work in the same area. Lange's observations agreed with Wedekind's (1914) revision in restricting *Genuclymenia* to $III\beta$, wherein it is abundant. Schindewolf's record of *G. frechi* from $III\alpha$ at Gattendorf is the only authentic occurrence of the genus known to the writer outside $III\beta$. Schindewolf's (1923, p. 435) record of *G. dunkeri* (Münster) from $V\alpha$ at Gattendorf refers to the type species of *Protoxyclymenia* Schindewolf 1922.

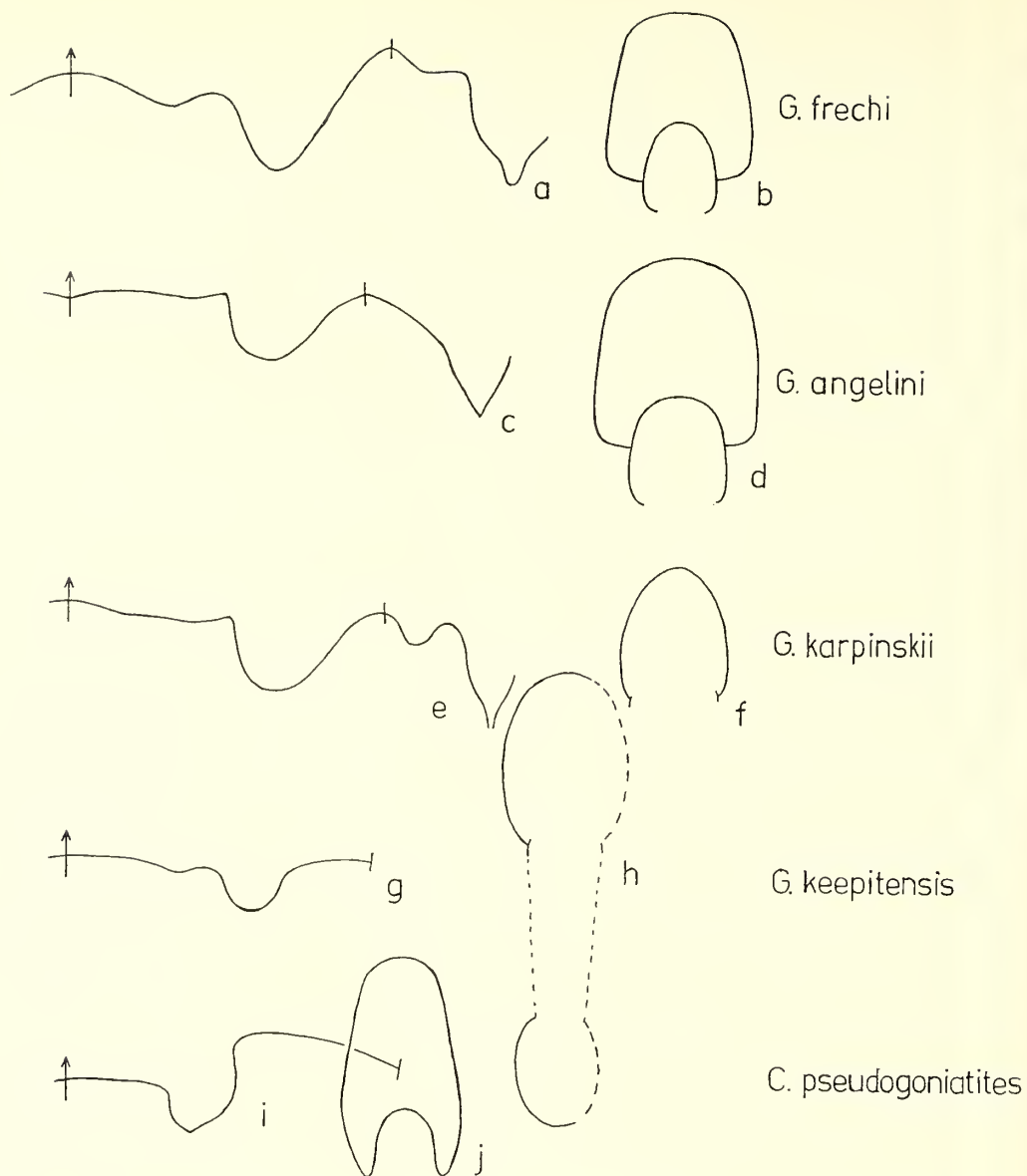
Family CLYMENIIDAE Edwards 1849

Genus PLATYCLYMENIA Hyatt 1884

Type species. By original designation *Goniatites annulatus* Münster 1832.

This genus receives the species of widely umbilicate clymenids having growth-lines which are concave on the lateral areas and simple sutures consisting of a broad ventral saddle passing evenly through a broadly rounded lateral lobe to a sharper, often angular umbilical saddle and a moderately deep, undivided dorsal lobe.

The genus is currently subdivided by Schindewolf (1934, 1957 in Moore) and Bogoslovsky (1962) into four subgenera: *P. (Pleuroclymenia)*, *P. (Trigonoclymenia)*, *P. (Spinoclymenia)*, and *P. (Platyclymenia)*, of which only the last is represented in my material. Species have been defined mainly on whorl section and ornamentation. It is well established that both characters change during the ontogeny of many included species. Specimens which combine the features of several nominal species are common (*vide* Lange 1929, pp. 93-6).



TEXT-FIG 1. Comparison of *G. keepitensis* sp. nov. with other species.

a, b, G. frechi Wedekind, the suture at maturity, from Schindewolf 1957 (text-fig. 40, 3b) and whorl section from Wedekind 1914, pl. 1, fig. 76.

c, d, G. angelini Wedekind, the suture from Perna 1914 (text-fig. 81) and whorl section from Wedekind 1914 (pl. 1, fig. 6b).

e, f, G. karpinskii (Perna), suture and whorl section from Perna 1914 (text-fig. 86a, and pl. 3, fig. 18a, respectively).

g, h, G. keepitensis sp. nov., suture $\times 6$, whorl section $\times 4$, based on holotype, USGD 6827.

i, j, C. pseudogoniaticites (Sandberger), suture and whorl section from Sandberger (1853, pl. 7, figs. 4b, 4a, respectively).

Platyclymenia is widespread in the northern hemisphere, being found in North America (U.S.A., Canada?), Europe, North Africa, and Asia (Kazakstan, China). It is also recorded from Western Australia (Teichert 1941) and a doubtful specimen from New South Wales has been figured by Pickett (1960).

Platyclymenia (Platyclymenia) annulata (Münster)

Neotype. By designation of Wedekind 1914: *Clymenia annulata* Münster; Gümbel 1863, pl. 15, fig. 12.

Diagnosis. A species of *Platyclymenia* with strong, sharp, unpaired, and clearly separated ribs on the flat or arched whorl sides; ribs absent or greatly reduced in later growth stages.

Remarks. Interpretation of this, the type species, was stabilized by Wedekind's selection of a neotype and clarified by Schindewolf's (1923) redefinition. Lange has discussed the morphological variation on the basis of material from around Enkeberg, close to the locality of the neotype and has described intergradations with *P. (P.) richteri* Wedekind which seemingly would be better regarded as a subspecies of *annulata*. Frech's (1902) *annulata* var. *densicosta* and Wedekind's (1914) *richteri* var. *densicosta* as well as Petter's (1960) *annulata* var. *semperornata* belong within the redefined species, but Perna's (1914) var. *correcta* and var. *rustica* are excluded.

Occurrence. Oberdevonstufe IV of Wedekind, more usually termed nowadays the *annulata* Zone, which is the uppermost division of the *Platyclymenia*-Stufe.

Platyclymenia (Platyclymenia) annulata annulata (Münster)

Plate 104, figs. 5, 6

- 1832 *Goniatites annulatus* Münster, p. 3, pl. 6, fig. 6 [fide auctt.].
 1834 *Goniatites annulatus* Münster; Münster, p. 95, pl. 6, fig. 6.
 1863 *Clymenia annulata* Münster; Gümbel, p. 130, pl. 15, fig. 12 [non figs. 11, 13].
 1910 *Clymenia annulata* Münster; Rzehak, p. 169, pl. 2, fig. 1 [non figs. 2-5].
 [non] 1914 *Clymenia annulata* Münst.; Perna, p. 75.
 1914 *Platyclymenia annulata* (Münster) Gümbel; Wedekind, p. 35.
 1923 *Platyclymenia annulata* Gümb. red.; Schindewolf, p. 447, pl. 17, figs. 7, 8.
 1929 *Platyclymenia annulata* Gümb. red. Schind.; Lange, p. 107.
 1956 *Platyclymenia (Platyclymenia) annulata* (Münster 1832); Müller, p. 70.
 1960 *Platyclymenia annulata* (Münster) 1832 red. Gümbel; Petter, p. 23, text-fig. 3E, pl. 4, figs. 4, 7, 9, 10.

Diagnosis. A subspecies of *P. (P.) annulata* having 26 or fewer ribs per whorl in the coarsely ribbed portion of the shell and a subrectangular or trapezoidal whorl section.

Material. Two specimens, one a fragment of an internal mould, the other two whorls of an internal mould and its external mould counterpart, preserved in a clayey sandstone.

Dimensions (in mm.)

	D	WW	WH	UW
USGD 6834 (internal mould)	63	—	c15	38

Description. The more complete specimen is large (maximum diameter over 88 mm.), widely evolute with a rounded rectangular whorl section in its strongly ribbed stage. The ribs are in the form of sharp ridges, radial to slightly prorsiradiate and weakly concave towards the aperture; they increase in height and width, but maintain their sharpness, towards the ventro-lateral shoulder and there flatten out abruptly, thus seemingly accentuating the sub-rectangular whorl shape. There are 21 ribs in the whorl ending at $WH = 9.5$ mm. Adjacent ribs are separated by completely smooth sections which are twice to four times the width of a rib. In the next whorl, ending with $WH = c. 15$ mm., the ribs are much less sharp, about twice as numerous and are highest towards the umbilical shoulder. The flank of the last preserved whorl, on the external mould, is smooth except for low radially elongate swellings which diminish in definition and elevation towards the aperture.

Part of one suture is preserved within the strongly ribbed stage; it shows the shallow, evenly rounded, lateral lobe which is characteristic of the genus.

Remarks. There is close correspondence with *P. annulata* red. Schindewolf and especially with a large specimen carefully described by Lange (1929, p. 111) under the name *Platyclymenia richteri*, but which he regarded as possibly belonging to *P. annulata*, presumably because the whorl section was not clearly observable.

Platyclymenia (Platyclymenia) annulata densicosta Frech

Plate 104, figs. 7, 8

- 1863 *Clymenia annulata* Münst. Gümbel, p. 130, pl. 15, fig. 13, 13a [non figs. 11, 12].
- 1902 *Clymenia annulata* var. *densicosta* Frech, p. 31, pl. 1, fig. 7.
- 1914 *Platyclymenia annulata* var. *densicosta* Frech emend.; Wedekind, p. 36, pl. 3, fig. 2.
- 1914 *Platyclymenia richteri* var. *densicosta* Wedekind, p. 35.
- 1923 *Platyclymenia annulata* var. *densicosta* Frech; Schindewolf, p. 449.
- 1929 *Platyclymenia annulata* var. *densicosta* Frech; Lange, p. 108.
- 1960 *Platyclymenia annulata* var. *densicosta* Frech emend. Wedekind; Petter, p. 24, pl. 4, fig. 5; pl. 5, figs. 13, 23.
- 1960 *Platyclymenia richteri* var. *semperornata* Petter, p. 25, pl. 4, figs. 6, 11.

Diagnosis. A subspecies of *P. (P.) annulata* having 27 or more ribs per whorl in the coarsely ribbed portion of the shell.

Material. Two specimens preserved in clayey sandstone, one a fragment of an external mould and the other an internal mould of two inner whorls.

Dimensions (in mm.)

	D	WW	WH	UW
USGD 6837 (internal mould)	21.7	c. 7	6.9	12.6

Description. The more complete specimen is a widely umbilicate small mould of approximately circular whorl section. Fourteen ribs in the last-preserved half whorl are sharp and are highest and broadest towards the venter, but abruptly end in a slightly prorsiradiate attitude to leave the venter unribbed and rounded. The inner of the two preserved whorls has somewhat more numerous but less sharp ribs.

The second specimen (USGD 6880) is a fragment of an external mould showing ten ribs of the *annulata* pattern in about one-third of a whorl.

Remarks. The close similarity of *P. (P.) annulata* and *P. (P.) richteri* in features other than whorl shape, and the existence of specimens of intermediate whorl section has been pointed out by Lange and Petter. Each species has a named variety distinguished from its type by more numerous ribs: *annulata* var. *densicosta* Frech and *richteri* var. *densicosta* Wedekind. In view of their similarity, intergradation, corresponding varieties and ranges I consider that *annulata* and *richteri* belong to one species and, further, that the more closely ribbed nominal varieties constitute a single taxon of subspecific rank which includes also Petter's var. *semperornata*.

In publishing the name var. *densicosta* Frech cited two specimens, one fragmentary (his pl. 1, fig. 7) and the other Gümbel's plate 15, fig. 15 (*sic*), which, as there is no fig. 15 or 14 on Gümbel's plate 15, must be read plate 15, fig. 13, and then corresponds with the text. The latter is a specimen of five whorls ending at WH = 8.5 mm, with 28 ribs in the last preserved whorl. I hereby designate it as lectotype of *P. (P.) annulata densicosta* Frech.

Platyclymenia (Platyclymenia) teichertii sp. nov.

Plate 104, figs. 9–13; Plate 105, figs. 1–4; text-fig. 2a–j

Derivation of name. For Professor Curt Teichert of the University of Kansas Paleontological Institute.

Syntypes. USGD. 6839, 6890, 6891.

Material and preservation. About forty more or less complete shells in clayey sandstone, crushed and decalcified to varying degrees.

Dimensions (in mm.)

	D	WW	WH	UW
USGD 6839	c. 42	(crushed)	13	21
USGD 6890	25	c. 5.5	6.9	13.0
USGD 6891	23	c. 5	5.6	13

Diagnosis. A species of *Platyclymenia* which is unribbed and very widely evolute, with an umbilical diameter equal to or greater than one-half the total diameter, i.e. $UW \times 2 \geq D$.

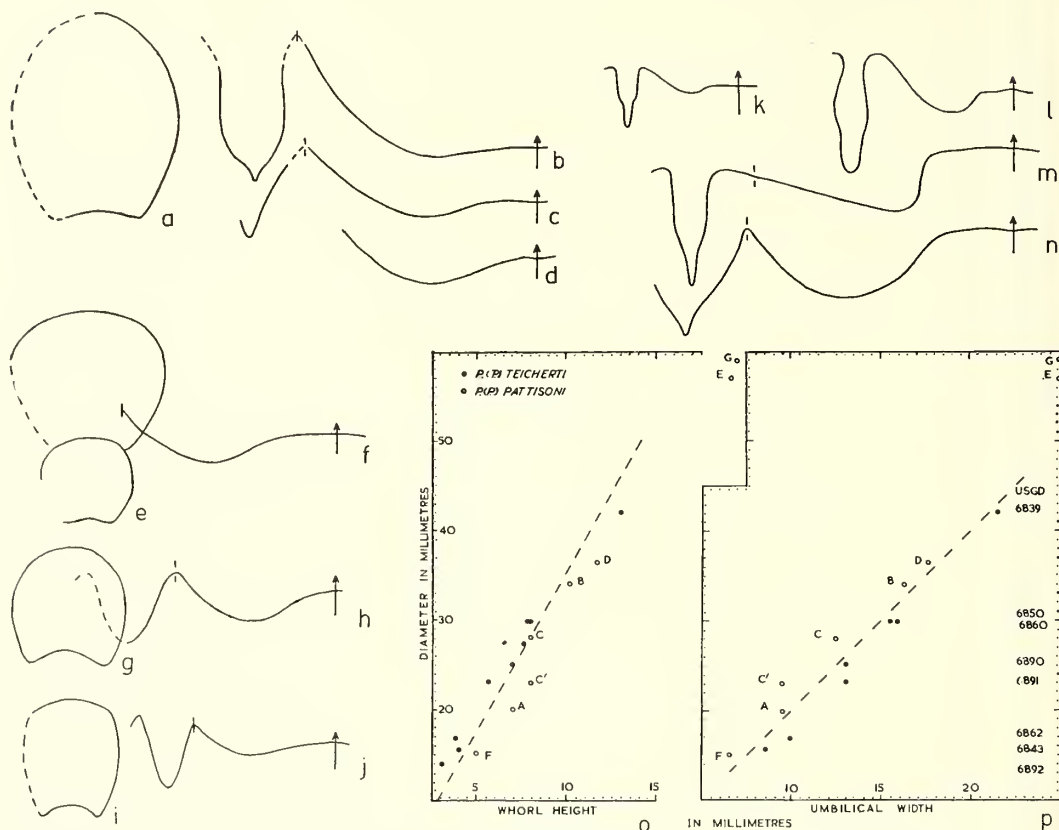
Description. The smooth widely umbilicate shells have whorls which vary in cross-section between sub-circular, oval and sub-rectangular; impressed area is always shallow (text-fig. 2).

Rarely preserved growth-lines are almost rectiradiate faint undulations showing a weak lateral sinus (Pl. 104, fig. 9); they have not been observed on the venter.

Suture lines consist of an almost flat ventral saddle, broad, evenly rounded lateral lobes, moderately sharp umbilical saddles, and a widely open dorsal lobe. The umbilical saddle is usually crested forward of the ventral saddle; in several specimens this forward projection of the umbilical saddles is accentuated in late growth stages (text-fig. 2b). One sectioned specimen shows septa near the dorsum to be strongly deflected forward to meet the next succeeding septum, and apparently failing to form complete transverse partitions; this curious configuration may possibly have resulted from distortion. In some specimens (e.g. USGD 6846) the curvature of the lateral lobe is localized on the mid-flank, forming a very broad V.

Septal necks are short.

Late growth stages usually show internal constrictions numbering up to 5 per whorl.



TEXT-FIG. 2. Comparison of *P. (P.) teichertii* sp. nov. with *P. (P.) pattisoni* (M'Coy) and *Clymenia laevigata* (Münster).

a-j, *P. (P.) teichertii* sp. nov. $\times 4$. *a-d*, based on USGD 6890; *a*, whorl section at $D = 24.3$ mm.; *b*, the last suture, at $D = 24$ mm.; last but one suture, at $D = 23.5$ mm.; last but four suture at $D = c. 20.5$ mm.; *e, f*, based on USGD 6891; *e*, whorl section, *f*, external suture, both at $D = c. 19$ mm.; *g, h*, based on USGD 6843; *g*, whorl section, *h*, suture, both at $D = c. 15.5$ mm.; *i, j*, based on USGD 6862; *i*, whorl section, *j*, suture, both at $D = 16.9$ mm.;

k-m, sutures of *C. laevigata*. *k*, copied from Sandberger, 1853, pl. 7, fig. 1e-f; *l*, copied from Gümbel, 1863, pl. 16, fig. 5c, 'Münster's Original'; *m*, copied from Bogoslovsky *et al.* in Orlov 1962, fig. 187a; *n*, suture of *C. placida* Perna, copied from Perna 1914, fig. 79.

o, whorl height plotted against diameter for *P. (P.) teichertii* and *P. (P.) pattisoni*.

p, umbilical width plotted against diameter for the same species. Specimens of *P. (P.) teichertii* represented in these diagrams are indicated by USGD numbers at the left margin. Represented specimens of *P. (P.) pattisoni* are indexed by letters A-G; A, holotype of *pattisoni*, dimensions from Selwood 1960, p. 165; B, C, *P. placida* from Perna 1914, p. 77; C, *P. subnautilina* from Petter 1960, p. 27; C¹ from Petter 1960, pl. 5, fig. 20; D, E, *P. quenstedti*, from Wedekind 1914, p. 45; F, *P. subnautilina schleizi* from Müller, 1956, p. 74; G, *C. subnautilina* from Sandberger 1855, pl. 1, fig. 1f.

They are rectiradiate to rursiradiate, straight or with a slight forward concavity, and are formed by wave-like thickenings which may be symmetrical or have crests located forward of their mid-line. Constrictions are not detectable externally.

Remarks. Smooth species of *Platyclymenia* are not always readily distinguished from species of *Clymenia*. Wedekind's criterion of relative straightness of growth-lines in *Clymenia* is unsatisfactory since they are rarely preserved in either group and may be nearly straight in late growth stages of *Platyclymenia* (Schindewolf 1923, p. 462; Müller 1956, p. 74). More practical are the criteria proposed by Schmidt (1924, p. 124) based on sutural and septal form: the wider dorsal lobe and shorter septal necks of *P. subnautilina* in comparison with *C. laevigata*. Suture diagrams showing dorsal lobes which are about as deep as they are wide have been figured also for several other species of *P. (Platyclymenia)*, (e.g. Perna 1914, figs. 71, 72, 77, 79 and Schindewolf 1934, fig. 12); in this characteristic they contrast sharply with the narrow parallel-sided dorsal lobe of *Clymenia laevigata* (e.g. Sandberger 1853, pl. 6, fig. 6; pl. 7, fig. 1; Gümbel 1863, pl. 16, fig. 5c; Frech 1902, text-fig. 4b). The relatively wide dorsal lobes and the short septal necks of the new species therefore assign it to *Platyclymenia*.

Nominal species of *Platyclymenia* having oval or round cross-section and lacking ornamentation have been justifiably synonymized by Selwood (1960) under the name *P. (P.) pattisoni* M'Coy 1851 who also refigured the holotype (pl. 26, fig. 10, not fig. 11 as stated in text). Perna's species *Clymenia placida* also belongs, at least in part, to *P. (P.) pattisoni* (cf. Schindewolf 1922, p. 124). But the new species described above differs from *pattisoni* in being more widely umbilicate and in its slower rate of increase of whorl height (text-fig. 2o and p). In these characters of general form, and in the presence of constrictions, *P. (P.) teichertii* resembles *C. laevigata*, but in the present material it does not reach the size of the latter species. It could be regarded as a possible ancestor of *Clymenia*.

Occurrence. Specimens of *P. (P.) teichertii* outnumber the total of all the other species in the fauna here described.

Platyclymenia (Platyclymenia) alterna sp. nov.

Plate 105, figs. 8–11

Derivation of name. Latin *alternus*, alternating, referring to the ribs.

Holotype. USGD 6838, the only specimen found of this species.

Preservation. Internal mould of segment of one whorl and the more complete external mould of two whorls, preserved in clayey sandstone.

Dimensions (in mm.)

	D	WW	WH	UW
Holotype, USGD 6838	23.5	4.5	c. 7	11

Diagnosis. A species of *Platyclymenia* with intercalated ribs and a subrectangular whorl section.

Description. The holotype is widely umbilicate with a high subrectangular whorl section. It is slightly distorted and WW as measured may be somewhat reduced thereby. Whorls

overlap only slightly, the impressed area being about 1 mm. deep at WH = 7 mm. Whorl sides are parallel and the venter is weakly arched.

Ribs are concave, projected and in two alternating sets, both ending at the ventro-lateral shoulder to leave the venter smooth. The ribs of the more prominent set are usually continuous across the flanks; they increase in height and width towards the venter and, to a lesser extent, towards the umbilical seam, so that the ribs are relatively weak in the middle portion of the whorl. Intercalated ribs are usually confined to the outer half of the whorl, but may occasionally appear weakly near the umbilical seam. Crests of adjacent ribs are about 1.5 mm. apart at WH = 7, the accentuated rib terminations being there about 0.5 mm. wide.

Remarks. Two other specimens from the type locality having high subrectangular whorl sections and umbonally accentuated ribs may belong to this species (USGD 6835 and 6881); both represent a growth stage which is later than is preserved in the holotype and so cannot be confidently identified until more complete material becomes available.

In whorl shape the species resembles *P. (P.) sandbergeri* and *P. (P.) walcotti*, but the intercalated ribs of *alterna* are distinctive.

Family RECTOCLYMENIIDAE Schindewolf 1923

Genus RECTOCLYMENIA Wedekind 1908

Type species. *Rectoclymenia roemeri* Wedekind 1908 by subsequent designation of Schindewolf 1957.

Rectoclymenia ? sp.

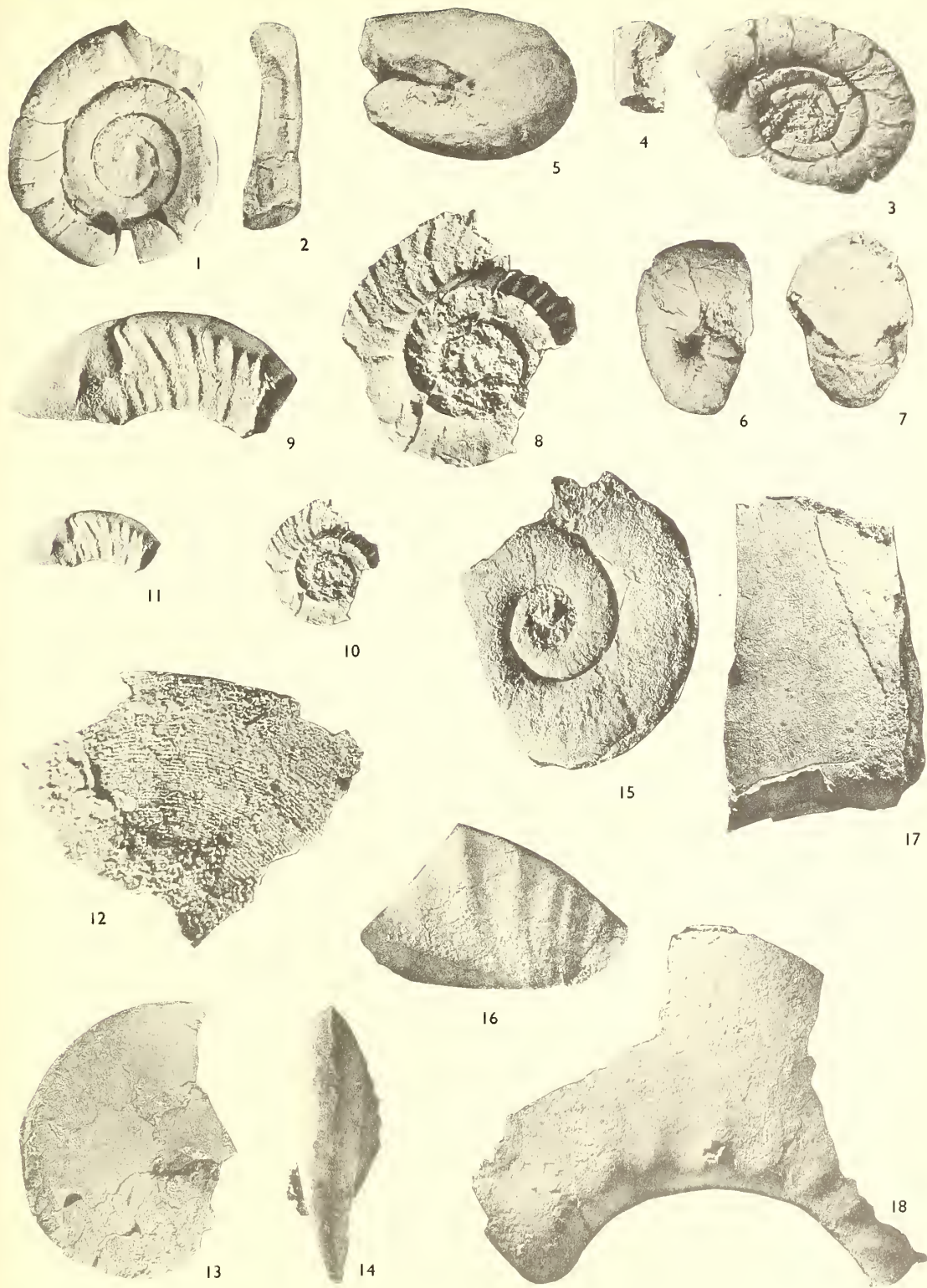
Plate 105, figs. 15–18

Description and remarks. Together with the other described species occur numerous fragments of a large coiled cephalopod. Its siphuncle has not been observed; the simple partial suture preserved on one fragment, the straightness of the low radial undulations on the whorl flanks and the general form suggest *Rectoclymenia*.

A quite exceptionally large size is indicated. One short portion of a whorl which is incomplete ventrally measures 74 mm. in the radial direction, has a whorl thickness

EXPLANATION OF PLATE 105

- Figs. 1–4. *P. (Platyclymenia) teichertii* sp. nov. 1, 2, internal mould, USGD 6862, $\times 2$; 3, 4, internal mould, USGD 6843, $\times 2$. 2, 4 are dorsal views of the detached incomplete body chambers showing septal face and internal suture.
- Figs. 5–7. *Sporadoceras* cf. *rotundum* Wedekind. 5, internal mould, USGD 6831, $\times 3$; 6, 7, internal mould, USGD 6832, $\times 3$.
- Figs. 8–11. *P. (Platyclymenia) alterna* sp. nov. 8, 9, external and internal moulds of holotype USGD 6832, $\times 2$; 10, 11, the same, $\times 1$.
- Figs. 12–14. *Sporadoceras inflexum* Wedekind. 12, part of impressed area of body whorl showing spiral striae, $\times 3$. 13, 14, lateral and ventral views, the latter showing the deformed venter, due to crushing; USGD 6866, $\times 1$.
- Figs. 15–18. *Rectoclymenia* ? sp. 15, small internal mould showing several partial sutures, USGD 6853, $\times 2$; 16, part of an external mould of an outer whorl photographed to show low rectiradial undulations, USGD 6899, $\times \frac{2}{3}$; 17, portion of an outer whorl, USGD 6865, $\times \frac{2}{3}$; 18, USGD 6864, $\times 1$.



(internal mould) of 24 mm. and an impressed area 12.5 mm. deep; its umbilical margin forms an arc which approximately fits a radius of 70 mm. A diameter of about 300 mm. is thus indicated.

Whorl section in late growth stages is compressed high oval, the very gently arched sides converging ventrally from the inner flanks to an evenly rounded unkeeled venter. Sculpture seemingly changes with growth from rectiradiate ribs, evenly rounded in profile and strongest towards the umbilicus, to low dorso-lateral bullae which pass radially into low rectiradiate swellings at a later growth stage. Faint radial growth lines parallel the ribs and also indicate a probable ventral sinus.

Three small unribbed specimens may represent an early growth stage. One shows simple sutures with shallow rounded lateral lobes (Pl. 105, fig. 15), is moderately evolute, and has the following dimensions (in mm.).

	R	WH	WW	UW
USGD 6853	12	6.7	c. 2	10

(WW may be reduced by compressive distortion).

Closest of the described species of *Rectoclymenia* in general form to these small specimens is *R. acuta* (Schmidt), but none is recorded as attaining the exceptionally large size indicated for the material described above.

According to Schindewolf (in Moore 1957) the genus is confined to the *Platyclymenia* Zone. It is previously recorded from Europe, Asia, and North America.

Suborder GONIATITINA Hyatt 1884
 Superfamily CHEILO CERATAEAE Frech 1897
 Family CHEILO CERATIDAE Frech 1897
 Genus SPORADOCERAS Hyatt 1884

Type species. Goniatites bidens G. and F. Sandberger by original designation.

Sporadoceras inflexum Wedekind

Plate 105, figs. 12–14; text-fig. 3a, b

- 1908 *Sporadoceras inflexum* Wedekind, p. 595, pl. 39, fig. 43; pl. 42, figs. 3, 3a.
 [non] 1914 *Sporadoceras inflexum* Wedekind; Perna, p. 36, 98, pl. 1, fig. 14; text-fig. 21 [= *S. muensteri* var *brachyloba* Frech]
 1918 *Sporadoceras inflexum* Wedekind; Wedekind, p. 149, text-fig. 47d.
 1959 *Sporadoceras inflexum* Wedekind; Petter, p. 274.

Material. One specimen (USGD 6866), an internal mould, somewhat crushed.

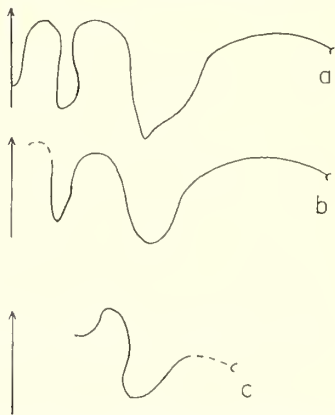
Diagnosis. A species of *Sporadoceras* in which the second lateral lobe is pointed and is two or three times as wide as the first lateral lobe which is shorter and skewed towards the venter.

Dimensions (in mm.)

	D	WW	WH	UW
USGD 6866 (internal mould)	45.8	11+	16	nil

Description. The mould shows a closed umbilicus, the whorls being completely overlapping; the body chamber extends through three-quarters of a whorl. Whorl section is interpreted as having been approximately oval with an evenly rounded venter; crushing has resulted in a narrowed venter but the original rounded venter is preserved at some points.

A detached fragment of the body chamber preserves a sector of its impressed area which clearly shows fine and regular spiral striae (about 30 per cm.).



TEXT-FIG. 3. Sutures of *Sporadoceras*. a, b, *S. inflexum* Wedekind, based on USGD 6866 at D = c. 47; $\times 2$. c, *S. cf. rotundum* Wedekind, based on USGD 6832 at D = c. 9; $\times 4.25$.

The suture is characteristic of the genus (text-fig. 3a, b) with rounded saddles and more or less pointed lobes. The inner lateral saddle is pointed and asymmetrical with a straighter outer limb; the outer lateral saddle is shorter, deep and narrow, parallel sided, ending bluntly or sub-acutely with a slight outward direction.

Remarks. The specimen described resembles *heterolobatum* Lange but its first lateral lobe lacks the consistent sharpness shown in Lange's species, and its first lateral saddle (E/A₁₁) is relatively higher. The ventral deflection of the first lateral lobe in my specimen, is less than in Wedekind's figure of the type of *S. inflexum*, but this is judged to have been possibly diminished by the partial crushing which has converted an originally rounded venter to an acute form.

S. muensteri var. *brachyloba* Frech and *S. pseudocarinatum* Petter are somewhat similar to my specimen in shell-form and suture but have a relatively wider first lateral lobe.

Sporadoceras inflexum, is previously recorded from III β in Germany and from an unrecorded locality and horizon in North Africa (Petter 1959).

Sporadoceras cf. rotundum Wedekind

Plate 105, figs. 5-7; text-fig. 3c

1908 *Sporadoceras rotundum* Wedekind, p. 594, pl. 39, fig. 21; pl. 42, fig. 1.

1918 *Sporadoceras rotundum* Wedekind; Wedekind, p. 148, text-fig. 47c.

Two similar small distorted specimens of *Sporadoceras* are comparable with *S. rotundum* in form and suture-line. The widely rounded venter and the dorso-ventral direction of distortion by compaction indicate an originally sub-sphaerical form. A partial external suture (text-fig. 3c) on the smaller specimen shows a deep and pointed second lateral lobe and a shallow rounded first lateral; the umbilical sector is indistinct but probably as shown by the dashed line, whereas the ventral sector is not observable. Both specimens show three constrictions about 90° apart; they are rectiradiate on the flanks and show a constant shallow rounded ventral sinus. *Sporadoceras biferum* is similar in its suture-line and has a named variety (*sulcifera* Lange) distinguished by

constrictions, but its shell-form is more compressed than that indicated for the specimens here recorded.

S. rotundum is recorded from Zones III α and III β in Germany and the lower *Prolobites* Zone (= III α) in the Urals. *S. biferum* is recorded from Zones II β –III β in Germany and Zones II–IV in the Sahara.

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T. B. H. JENKINS

Department of Geology and Geophysics
The University of Sydney
Sydney, N.S.W.
Australia

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AQUILAPOLLENITES IN THE BRITISH ISLES

by A. R. H. MARTIN

ABSTRACT. Species of *Aquilapollenites* Rouse emend. Funkhouser are present in the interbasaltic lignites of Shiaba and Bremanoir, Mull, Scotland. The bearing of this on the age of the lignites is discussed; it is believed that this may be pre-Eocene.

THE genus *Aquilapollenites* Rouse (1957) emend. Funkhouser (1961) has been regarded as an important indicator pollen fossil of the uppermost Cretaceous, Palaeocene, and Lower Eocene of parts of the Northern Hemisphere, at least Western and Plains states of North America and North-west and Central Siberia. Funkhouser (1961) and Stanley (1961) refer to the lack of records of the genus from western Europe. However, at about the same time, a posthumously published paper by J. B. Simpson (1961) described the genus *Taurocephalus* as new and ascribed to it the single species *T. proteus*, which was regarded as an extinct member of the Proteaceae. This very characteristic pollen is clearly *Aquilapollenites*, but as the description differs somewhat from the published description of *Aquilapollenites*, a brief explanation is offered.

Simpson apparently saw in polar view, the fine furrows which in *Aquilapollenites* have been described as demicolpoids, but interpreted these as a proximal-face triradiate mark such as he believed to occur in some Proteaceae. The two polar lobes of the grain (Pl. 106, fig. 6), superimposed one over the other, appear to have been taken for a single distal pore resembling the three equatorial protrusions which were also described as pores. These were correctly described as differing from all extant Proteaceae in that ectexine covered the supposed pores. Simpson's own photographs (1961, pl. xii, figs. 1, 2, and 5, for example) show that two polar protrusions are present. *Taurocephalus* is described as sometimes having four equatorial arms; this is the only way of reconciling the appearance of Simpson's figs. 1 and 5 with his description since these are equatorial views. However, his plate xii, fig. 11 is a specimen with four true equatorial arms seen in polar view. The specimen has been re-located and re-photographed (Pl. 106, figs. 1-3). This feature had not been observed before in *Aquilapollenites*. Four-armed grains are probably of low incidence.

In examining the material from Mull, in which *Aquilapollenites* occurs, a second species and a few grains of a third were observed. Indeed *Taurocephalus proteus* is likely to be a compound of two of these species (see taxonomic section). To find these in sediments believed to be of Miocene or Pliocene age (the interbasaltic lignites of Shiaba and Bremanoir) suggests that the dating of the lignites should be reconsidered. An age between Maastrichtian and Lower Eocene seems most likely. The reliance on high percentages of coryloid, quercooid, and Hamamelidaceae-type pollens seems misplaced when it is realized that these pollens have a very extended time range. Manum (1962), for example, reports many such grains in the Tertiary of Vestspitsbergen, which on zoological grounds is thought to be late Palaeocene to Eocene. British phytogeographers, reluctant to accept the Mull interbasaltics as contemporary with the London Clay

flora, would probably be sympathetic towards the earlier rather than the later end of the range in time indicated by *Aquilapollenites* i.e. uppermost Cretaceous rather than Eocene.

Several other pollen grain types present in the interbasaltic beds are consistent with the earlier dating here proposed. These include *Classopollis* sp. (Pl. 106, figs. 15–16), which though uncommon, does not show any obvious signs of redeposition and, in lignite, is less likely to be re-deposited. The known range is Triassic to Eocene but it is uncommon after the mid-Cretaceous. *Haloragis bremanoirensis* Simpson is conspecific with *Nudopollis thiergartii* Pflug, an indicator of the Palaeocene in Germany, though ranging from the Maastrichtian to Lower Eocene.

A search for *Aquilapollenites* on slides, prepared by Simpson, of the pre-basaltic lignite of Ardslish, Ardnamurchan, failed to reveal any. All the slides quoted in the paper of 1961 were re-examined. Most were in fair condition, with pollen grains still stained by safranin, though some had developed small crystals in the glycerine jelly mountant.

SYSTEMATIC DESCRIPTION

ANGIOSPERMAE *Incertae sedis*

Genus AQUILAPOLLENITES Rouse emend. Funkhouser (April 1961)

Taxonomic synonymus. *Parviprojectus* Mchedlishvili (July 1961); *Taurocephalus* Simpson (December 1961).

Aquilapollenites spinulosus Funkhouser (*Taurocephalus proteus* Simpson pro parte)

Plate 106, fig. 7

Size range (10 grains). Polar axis 35–43 μ (av. 38 μ); tips of equatorial projections to polar axis 19–25 μ (av. 23 μ); (ratio 0.5–0.67).

Location. Bremanoir and Shiaba interbasaltic lignites, Mull, Scotland.

Known time range. Palaeocene–Eocene (Funkhouser 1961); Maastrichtian (Srivastava 1966).

Aquilapollenites attenuatus Funkhouser (*Taurocephalus proteus* Simpson pro parte)

Plate 106, figs. 1–6

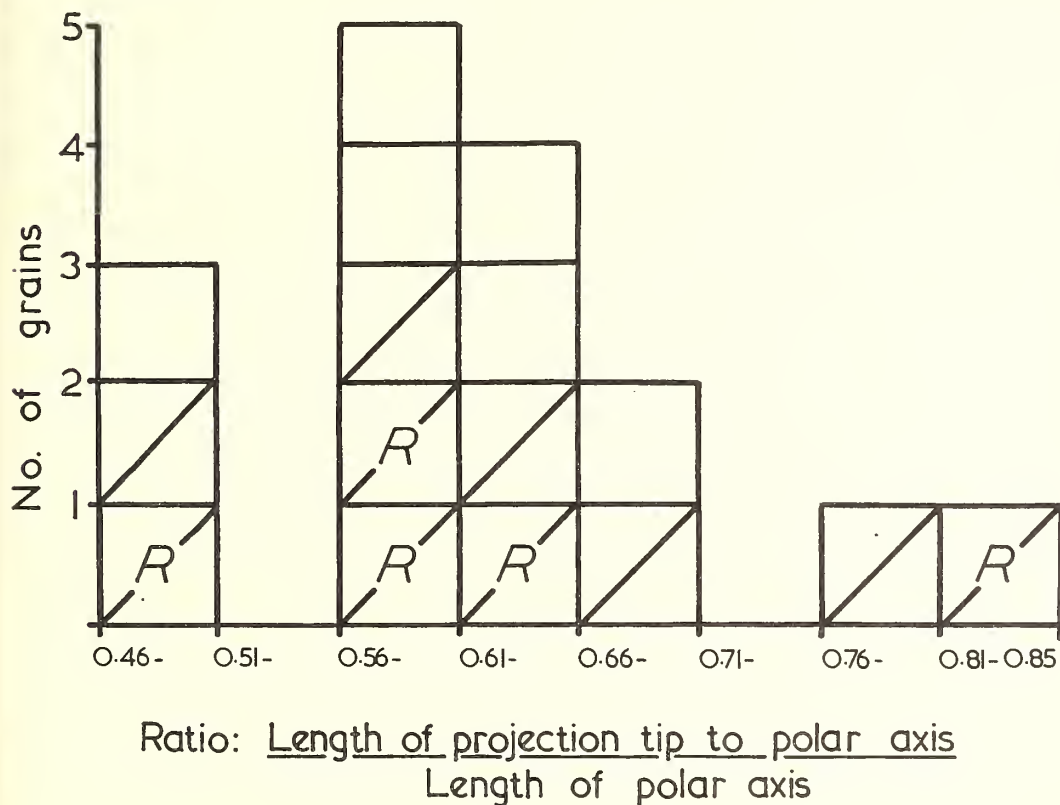
Size range (5 grains). Polar axis 28–42 μ (av. 36 μ); tips of equatorial projections to polar axis 21–24 μ (av. 23 μ); (ratio 0.5–0.8). Four-armed grains are of rare occurrence.

Location. Bremanoir and Shiaba interbasaltic lignites, Mull, Scotland.

Known time range. Maastrichtian (Funkhouser 1961, Srivastava 1966).

Distinction. The characters held to distinguish *A. spinulosus* from *A. attenuatus* are the shorter equatorial protrusions, the absence of puncta and the scattering of spinules over the whole surface instead of being grouped. In the Scottish material, while it is possible to find specimens corresponding to the two forms, there are a good many which combine features of both (text-fig. 1). The term ‘punctate’ could be applied to 70% of the Mull specimens, including both long and short-armed ones and to some with scattered

as well as those with grouped spinules. It is too early to suggest that a single polymorphic form is represented, but clearly there is a need for further study of the variability shown by these forms.



TEXT-FIG. 1. Number of *Aquilapollenites spinulosus* and *A. attenuatus* grains falling into different polar length/equatorial radius classes. Crossed squares = punctate grains. R indicates grain with spinules restricted to parts of surface.

Aquilapollenites pachypolus nom. nov.

Plate 106, figs. 8-14

Nomenclatural synonym. *Parviprojectus striatus* Mtchedlishvili 1961, pl. 73, fig. 1a-c. The genus *Parviprojectus* is a later homonym of *Aquilapollenites* as emended by Funkhouser and within that genus the name *striatus* is preoccupied by *A. striatus* Funkhouser. It is therefore necessary to give a new name to this very distinctive form. A translation of Mtchedlishvili's diagnosis and description of *Parviprojectus striatus* follows:

Diagnosis. Pollen grains rather large sized, tricolpate. Body broadly ellipsoidal in form, equatorial projections short, colpi resembling cracks. Exine thick, pilate, striate, but having thickenings on the polar areas.

Description. Length of grain 46.0–46.6 μ ; diameter of body 27.4–31.0 μ , length of equatorial projections 9.7 μ , their width 7.7–9.0 μ .

Pollen grains tricolpate. Outline of body in equatorial view broadly ellipsoidal. Exine thickness about 2.0 μ . Nexine layer only slightly thinner than sexine layer, tapering from the proximal end of the projection. Sexine consisting of pila which have grown together to form comb-like lirae. In sectional view are seen the thinner parts of the columns and the round heads. The lirae are situated at a slight angle to each other and sometimes branch, forming the characteristic striate structure of the grain. At the poles the sexine layer becomes considerably wider, forming thickened polar areas which have a corrugated structure. On the equatorial projections the sexine layer becomes considerably thinner. Colour of grains brown.

Size range of Scottish specimens (5 grains). Polar axis 35–43 μ (av. 40 μ); equatorial axis 28–33 μ (c. 38 μ tip to tip of protrusions); thickness of the polar area 4.5–6.0 μ .

Location. Shiaba interbasaltic lignites, Mull, Scotland.

Known time range. Maastrichtian–(?) Danian (Samoilovich and Mtchedlishvili 1961).

Distinction. The grains are distinguishable from *A. murus* Stanley, and *A. bertillonites* Funkhouser by the thickened polar areas. They are partially distinguishable by their generally larger size and shorter projections. The colpoids are very narrow, rather indistinct, and in one specimen (Pl. 106, fig. 10), pores appear to be present. The size of Scottish specimens is smaller than in the two Siberian specimens.

EXPLANATION OF PLATE 106

Magnification of all figures, $\times 1,000$.

Figs. 1–3. *Aquilapollenites attenuatus* Funkhouser (*Taurocephalus proteus* Simpson pro parte). Specimen with four equatorial arms, also showing demicolpi; slide Bremanoir 5a (= Simpson 1961, pl. xii, fig. 11). 1, High focus, polar area. 2, High focus, exine pattern, showing baculi (puncta) and spines. 3, Low focus, exine pattern (LO-pattern).

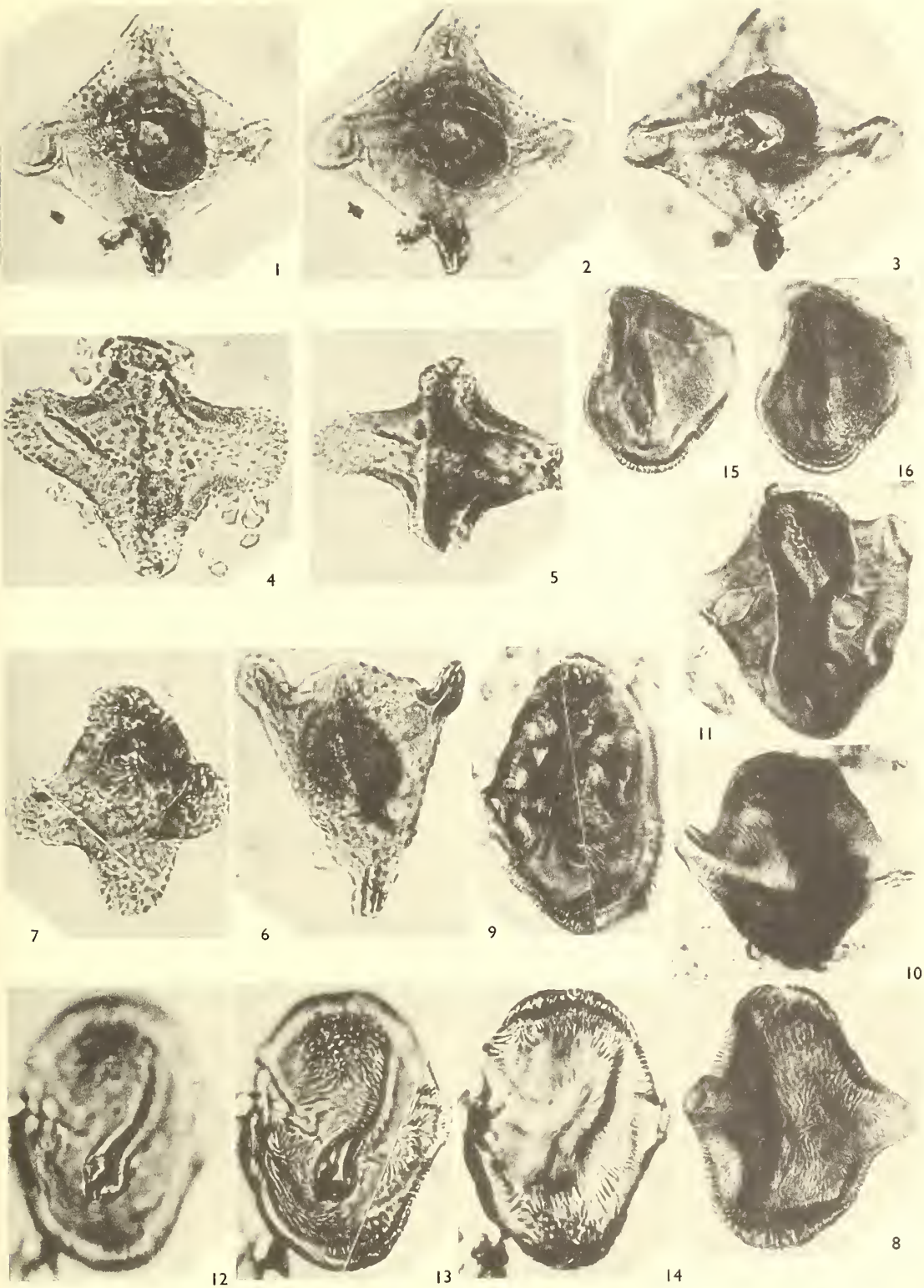
Figs. 4–6. *Aquilapollenites attenuatus* Funkhouser. 4, Equatorial view, showing well-defined double pattern of spines and baculi (LO-pattern); slide Shiaba 29a. 5, Equatorial view of small grain showing typical *attenuatus* shape, but lacking distinct LO-pattern; slide Bremanoir 5a. 6, Polar view; slide Bremanoir 5a.

Fig. 7. *Aquilapollenites spinulosus* Funkhouser (*Taurocephalus proteus* Simpson pro parte). Equatorial view, showing scattered spines and lack of distinct LO-pattern; slide Bremanoir 5a.

Figs. 8–14. *Aquilapollenites pachypolus* nom. nov. (*Parviprojectus striatus* Mtched.). 8, Equatorial view, showing striate pattern, short projecting arms, and thickened polar area; slide Shiaba 1a. 9, Surface and median view to show thickening of both ectexine and endexine in polar area; slide Shiaba 22a. 10, Small grain, with apparent pore-apertures on equatorial arms, showing some convergence towards *A. bertillonites* Funkhouser; slide Shiaba 22a. 11, Oblique view, sculpture of polar area insuluous, colpoid visible in facing projection; slide Shiaba 1a. 12–13, Successive views through specimen with upward projecting arm, showing the continuation of the striate pattern over the narrow indistinct colpoid, thus demonstrating that the colpoid is restricted to the endexine. 14, The same, focused on pattern of lower surface of grain; slide Shiaba 36f.

Figs. 15–16. *Classopollis* sp. High and low focus of striate exine surrounding pore, which faces to right; slide Shiaba 1a.

All photographs from original slides prepared by J. B. Simpson, and housed in Scottish Geological Survey Office, Edinburgh.



MARTIN, *Aquilapollenites* from Scotland

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A. R. H. MARTIN
School of Biological Sciences
University of Sydney
Australia

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DISCOHELIX (ARCHAEOGASTROPODA, EUOMPHALACEA) AS AN INDEX FOSSIL IN THE TETHYAN JURASSIC

by J. WENDT

ABSTRACT. Morphological features, growth, mode of life, and stratigraphical distribution are examined in more than 300 extremely well-preserved specimens of *Discohelix* from the Sicilian Lower and Middle Jurassic. In some species parabolic ribs similar to those in ammonites are formed owing to resorption during brief discontinuities in growth. Deviated peristomes recurring at an angle of more or less 72° and resulting in a pentagonal outline of the shell, are developed in two species for which the new subgenus *Pentagonodiscus* (type species *D. (P.) angusta* n. sp.) is established. Ten species of *Discohelix* sensu stricto are described, five of which are new: *D. dictyota*, *D. conica*, *D. centricosta*, *D. costata*, and *D. levis*. The short stratigraphical ranges of the representatives of the genus are proved here for the first time and may be useful for the division of cephalopod-free series in the Tethyan Jurassic.

FEW genera of the widely distributed Palaeozoic Euomphalacea crossed the Permo-Triassic boundary and the superfamily became extinct in the Upper Cretaceous. In contrast to its Palaeozoic representatives, amongst which Knight (1934, p. 145) was even able to recognize some with value as index forms, those in the Mesozoic have neither been investigated in quantity nor in relation to their stratigraphical occurrence. Both these omissions can now be corrected using an individually and specifically rich gastropod fauna from the Jurassic of Sicily, of which members of the genus *Discohelix* are the chief element. The accompanying ammonites have usually allowed all the specimens to be zonally dated, so far as strong condensation permits such accuracy. A total of more than 300 *Discohelix*, extremely well preserved and with complete shells, have been collected from several Jurassic sections in western Sicily (Rocca Busambra). The only drawback is the recrystallization of the shell material which has left its structure difficult to recognize. Several specimens from the Liassic of the Northern Calcareous Alps, the originals of Stoliczka (1861) from the north alpine Hierlatz facies, and those of Quenstedt (1884) and Brösamlen (1909) from the south German epicontinental Jurassic have been available for comparison.

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MORPHOLOGY

Protoconch

Because of the more or less planispiral coiling of the shell, the larval whorls are almost always preserved, so that the sculpture of the earliest ontogenetic stages can be precisely

followed. After the nucleus, which is always smooth, two or three fine spiral lines appear on the upper and lower sides in the majority of the investigated individuals. After one or two whorls they disappear even if a renewed spiral ornament occurs later on the teleoconch (Pl. 107, fig. 16). In only three species is the protoconch completely smooth (Pl. 107, fig. 15). A boundary between the proto- and teleoconch can neither be traced through a particularly accentuated interruption in growth (varix), nor through a sudden onset of the adult sculpture. The number of larval whorls can therefore not be determined. When the shell is biconcave the protoconch is commonly slightly raised (text-fig. 3o), and when convexo-concave a little depressed (text-fig. 3c).

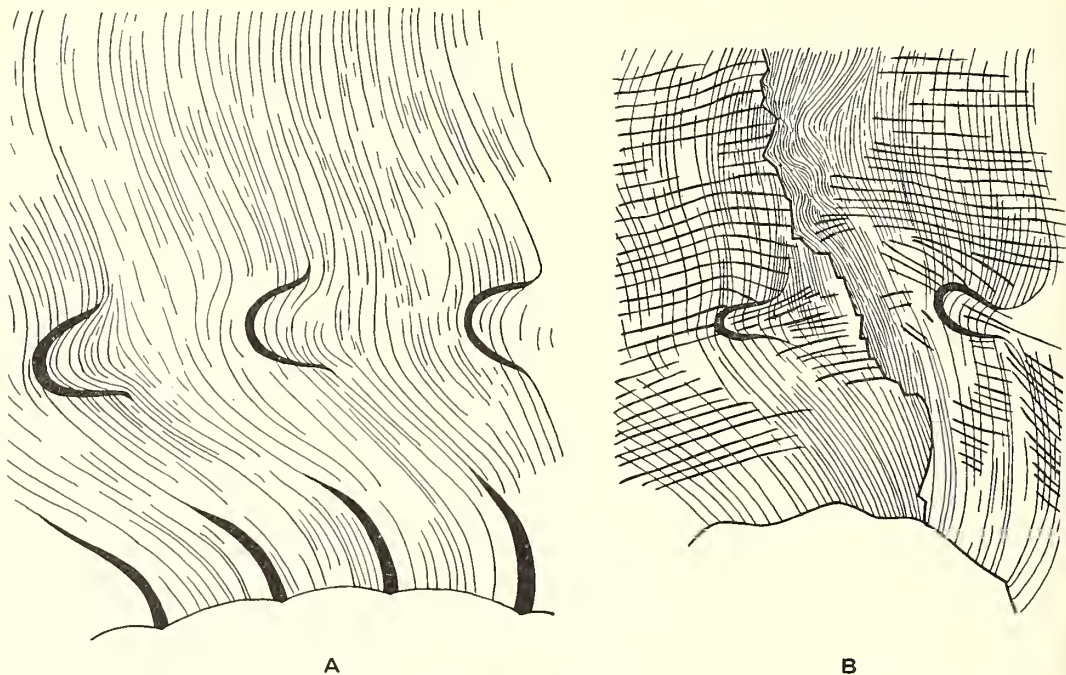
Teleoconch

Simple ribs. After one or two whorls, ribs appear more or less contemporaneously with the onset of clear growth-lines. They consist at first of weak swellings in the keel region, but with progressive growth they become enlarged as periodic ridges reaching to the suture on the upper and lower side, and running parallel with the growth-lines. On the interior of the shell this sculpture is either totally unreflected or only barely detectable, so that steinkerns of strongly ribbed forms may be perfectly smooth. As the growth-lines are not noticeably denser on the ribs themselves than between them, they are more likely to have been produced by periodically increased shell deposition than by a deceleration of growth. The number and strength of the ribs can vary considerably and is therefore of only restricted specific value.

Parabolic ribs. Long known in certain ammonites (especially perisphinctids) the significance of so-called parabolic ribs has often been discussed. In both ammonites and gastropods they are morphogenetically distinguishable from simple ribs. In form they are similar to simple ribs, but the course of the growth-lines is different. At regular intervals a growth-line (parabolic line) swings backwards in the keel region forming a parabolic notch and truncating the earlier growth-lines (text-fig. 1A). This is even more clearly seen on shells with a spiral sculpture since the sculpture itself is also cut off in the area of the parabolic notch. To some extent the spiral elements curve in sympathy with the notch and thus hint at the following discontinuity in growth (text-fig. 1B). The parabolic notch may be developed as a shell ridge (*D. albinatiensis*), or as a node (*D. cf. gümbeli*), or may take the form of a longitudinally open spine (*D. (P.) angusta*). In the last case the growth-lines are practically continuous.

The truncation of earlier growth-lines and the development of special sculpture features show that the normal growth of the shell was interrupted at these points. The finger-like protrusions of the mantle concomitant with the parabolic nodes or notches possessed the ability, on the one hand for resorption, and on the other, for shell secretion. As is often the case with the siphon it may have projected beyond the calcareous envelope which it deposited. In normal shell formation the parabolic notch was first closed before new material was added to the shell margin. Only then did a marked cessation of growth occur, since: firstly, in *D. (P.) angusta* the end of a strong inner varix (former peristome) does not lie immediately beneath the parabolic notch but shortly mouthwards of it; secondly, the existing peristome was only formed after the infilling of the parabolic notch (however, in this final growth stage the last 2–3 ribs are often simple); and thirdly, a clear concentration of growth-lines owing to decelerated growth is only

visible immediately after the parabolic line. In this area shell damage which affected the earlier peristome is often found (text-fig. 1B).



TEXT-FIG. 1. Parabolic nodes and course of the growth-lines from the suture to the middle of the outer side (raised parts of the shell in black). A. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/14, $\times 13$. B. *Discohelix* (*Pentagonodiscus*) *augusta* n. sp., with healed injury in a former peristome, Ga 1347/50, $\times 12$, 5.

From this it can be concluded that the parabolic notch may not itself be equated with a former aperture, in other words, a halt in growth (of course, strictly speaking each growth-line, and therefore also the parabolic line, represents a temporary shell margin). It is rather a part of a not wholly continuous process of shell secretion between two protracted interruptions in growth, although locally the contrary, namely resorption, occurs. Observation of recent gastropods has shown that shell secretion between two varices occupies only a few days and that a long pause follows thereafter, in which the peristome is only strengthened by internal varices or ribs (Fretter and Graham 1962, p. 64). For this reason gastropods in which the shell margin lies within the rapid growth phase are rarely found. The same growth process explains why a parabolic line has never been observed as the final peristome in ammonites. As the extension of the mantle withdrew the parabolic notch which it had produced was infilled, a process that bearing in mind the speed of growth in gastropods could probably have been completed within a few hours. Only later was growth interrupted, which in perisphinctids is commonly indicated by deep constrictions equivalent to the inner varices of gastropods. It remains unknown whether the temporary finger-like extensions of the mantle had a

physiological function in addition to the formation of parabolic notches and hollow spines. Nothing is known of this in gastropods either.

The interpretation of the parabolae of perisphinctids given by Schairer (1967, p. 26) is incorrect. He proposed as an explanation that 'the shell at certain points was more slowly deposited than at others' (author's translation). If such were the case the growth-lines would be of different density around the curve of the parabolic notch, but this is not so. Moreover, from Schairer's fig. 11, one can see that on the parabola the sculpture (in this case ribs as the author had only steinkern material) is indeed truncated. To my knowledge only Schindewolf (1934, p. 342, text-fig. 9) has demonstrated that the parabolae of ammonoids (here Upper Devonian clymenias) originated through local resorption.

Spiral ornament. Beginning with an intermediate growth-stage, commonly on the last 2–3 whorls, fine spiral lines are formed as result of a folding of the mantle edge. They appear first in the keel region and gradually encroach onto the sides, and together with the growth-lines and ribs produce a retiform sculpture typical of many gastropods. Their number and strength may vary considerably between specimens of equal dimensions, and spiral lines are therefore of only restricted value in the differentiation of species of *Discohelix*. For example in the case of *D. albinatiensis* they can be either equally spaced over the visible part of the whorl or only developed in the keel region, and thus show a transition to specifically inseparable shells without any spiral ornament (*D. cf. albinatiensis*).

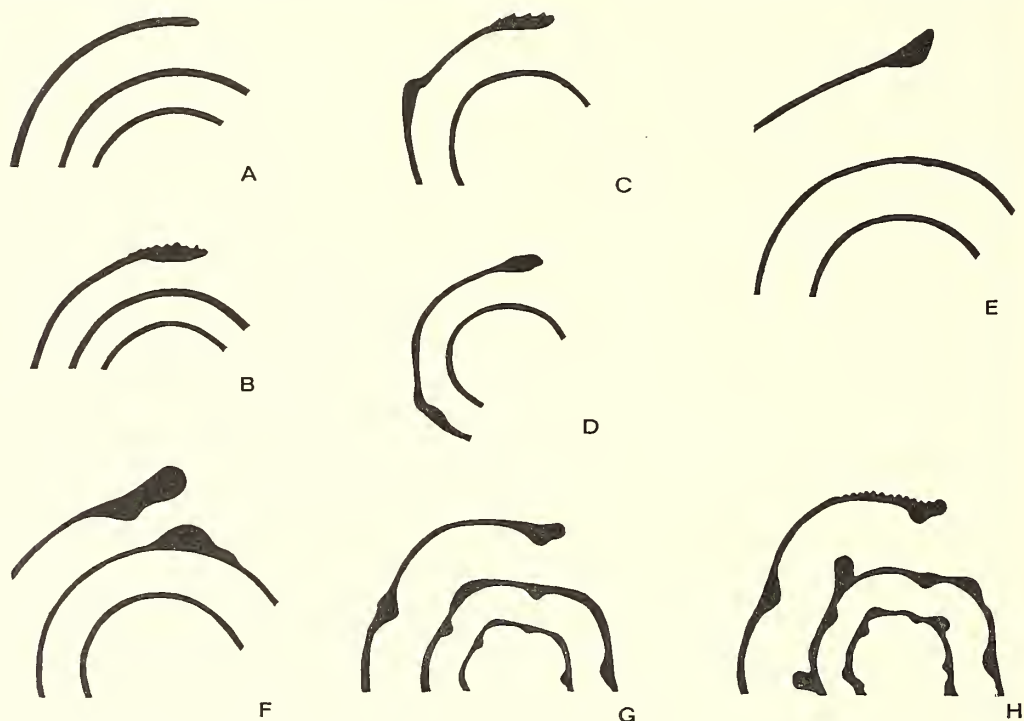
Peristome (text-fig. 2). Owing to the pure calcareous facies from which the whole of the material was collected, in no specimen could the peristome be completely cleared and the structures on the inside of the shell made visible. They could only be investigated in section, and the various types are best illustrated when cut in a longitudinal direction.

In the simplest case the shell margin can only be recognized through a marked concentration of the growth-lines, without any alteration of the peristome profile (e.g. *D. dictyota*, text-figs. 2A, 3E). Probably not to be specifically separated from this type is a peristome which is gradually thickened by the addition of new shell substance on the inner side, and which therefore appears somewhat narrowed in cross-section (e.g. *D. albinatiensis*, *D. conica*, *D. cf. crenulata*—text-figs. 2B, 3B, D, G, C). It may be preceded on the last whorl by one or two similar deposits formed during a pause in growth, but their position is random (text-figs. 2C, D).

The broadened, trumpet-like peristome is strengthened by an inner varix on the outer lip (e.g. *D. levis*, text-fig. 2E, 3L), and the aperture may also be narrowed by an inner varix on the inner lip (e.g. *D. cotswoldiae*, text-fig. 2F). The highest degree of specialization is achieved when these last two aperture types are repeated at regular intervals (*D. (P.) reussii* and *D. (P.) angusta*—text-figs. 2G, H).

Cross-section (text-fig. 3). A cross-section passing exactly through the protoconch illustrates best the considerable variety of form within *Discohelix*. The mean spiral angle may lie between the wide boundaries of 125° to 220°, and the mean umbilical angle between 65° and 145°. The comparison of these two angles in one specimen, and the weak trochospiral coiling of the protoconch, show that perfect bilateral symmetry is not

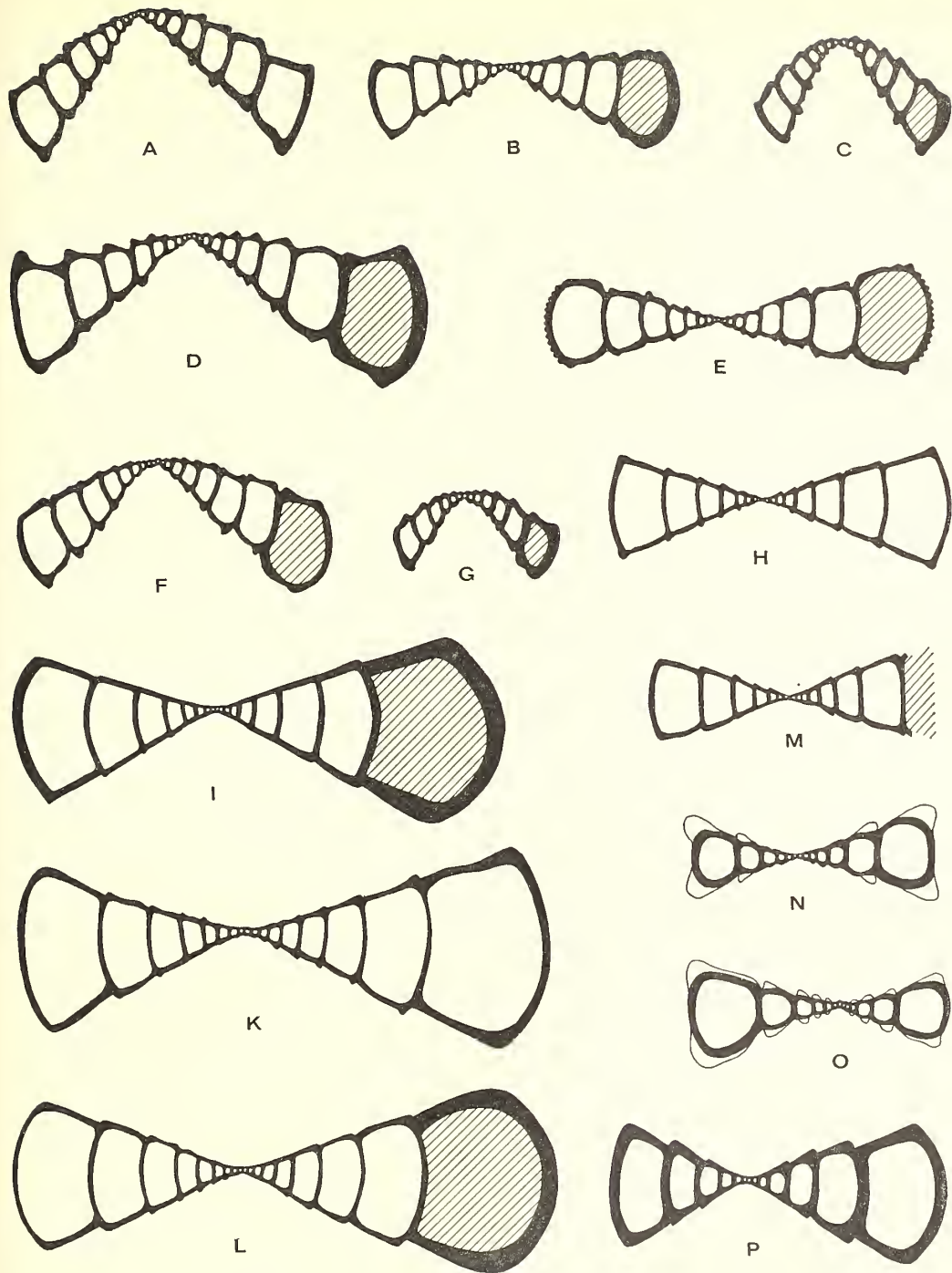
achieved in *Discohelix*. Transitions exist between a slightly concave, a plane, and a convex spire, so that this character cannot always be given specific significance. *D. albinatiensis* shows the greatest variability in this way and may occur with a plane (sometimes even slightly concave) to a clearly convex spire (text-figs. 3B, A). In one and the same individual



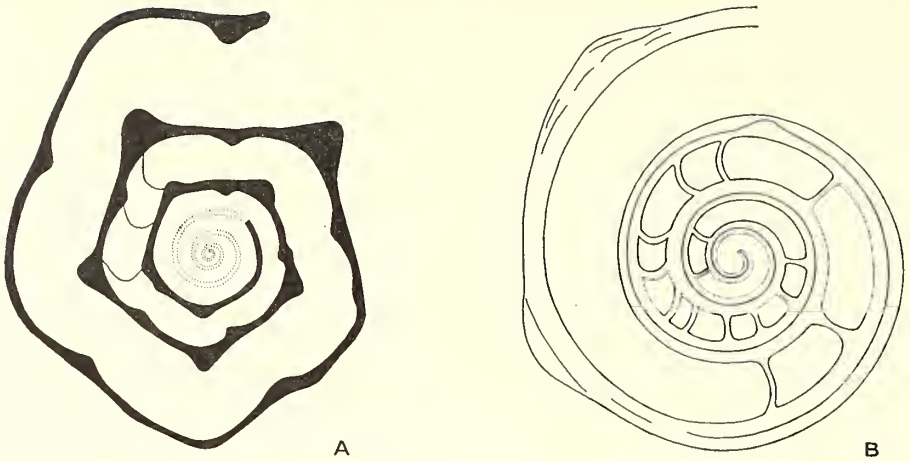
TEXT-FIG. 2. Types of peristomes (longitudinal sections), $\times 3$, 1. A. *Discohelix* (*D.*) *dictyota* n. sp., Ga 1347/4. B. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/12. C. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/28. D. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/29. E. *Discohelix* (*D.*) *levis*, n. sp., Ga 1347/41. F. *Discohelix* (*D.*) *cotswoldiae* (Lycett), Ga 1347/48. G. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnes, Ga 1347/56. H. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp., Ga 1347/51.

the degree of involution may change so that the cross-section loses its axial (mirror-image) symmetry.

Septa. Septa closing off the uninhabited parts of the shell were shown by Knight (1934, p. 140) to be typical for the Euomphalidae. However, although many longitudinal sections were prepared for the species investigated here, septa were observed in only a few cases. They were found in the first 2–3 whorls but showed no regularity in either number (3–15) or distance from one another (text-fig. 4B). In one specimen of *D. (P.) angusta* three septa were found lying against the inner varices towards the end of the penultimate whorl (text-fig. 4A). This very late deposition of septa is surprising and permits no generally applicable conclusion about the length of the visceral mass.



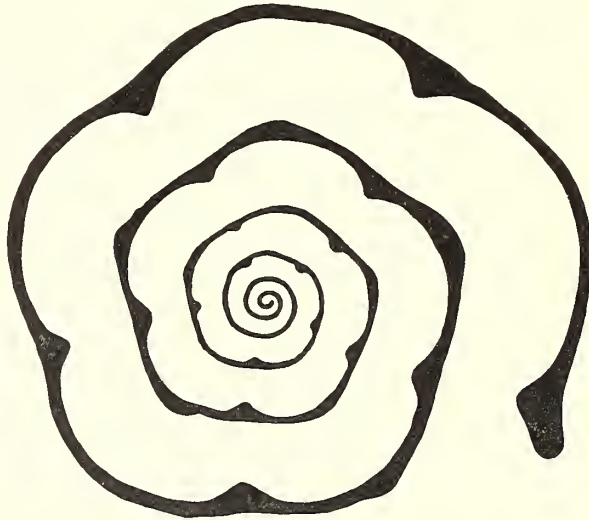
TEXT-FIG. 3. Cross-sections, $\times 3$, 1. A. *Discohelix* (D.) *albinatiensis* Dumortier, Ga 1347/9. B. *Discohelix* (D.) *albinatiensis* Dumortier, Ga 1347/7. C. *Discohelix* (D.) *conica* n. sp., Ga 1347/24. D. *Discohelix* (D.) cf. *albinatiensis* Dumortier, Ga 1347/15. E. *Discohelix* (D.) *dictyota* n. sp., Ga 1347/2. F. *Discohelix* (D.) cf. *crenulata* (Moore), Ga 1347/19. G. *Discohelix* (D.) cf. *crenulata* (Moore), Ga 1347/23. H. *Discohelix* (D.) cf. *calculiformis* Dunker, Ga 1347/42. I. *Discohelix* (D.) *centricosta* n. sp., Ga 1347/31. K. *Discohelix* (D.) *costata* n. sp., Ga 1347/35. L. *Discohelix* (D.) *levis*, n. sp. Ga 1347/37. M. *Discohelix* (D.) *cotswoldiae* (Lycett), Ga 1347/45. N. *Discohelix* (D.) cf. *gümbeli* Ammon, Ga 1347/49. O. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp., Ga 1347/52. P. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnes), Ga 1347/55.



TEXT-FIG. 4. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp. A. Ga 1347/54, longitudinal section with three septa towards the end of the penultimate whorl (inner whorls not preserved), $\times 3.2$. B. Ga 1347/51, inner whorls with septa, $\times 25$.

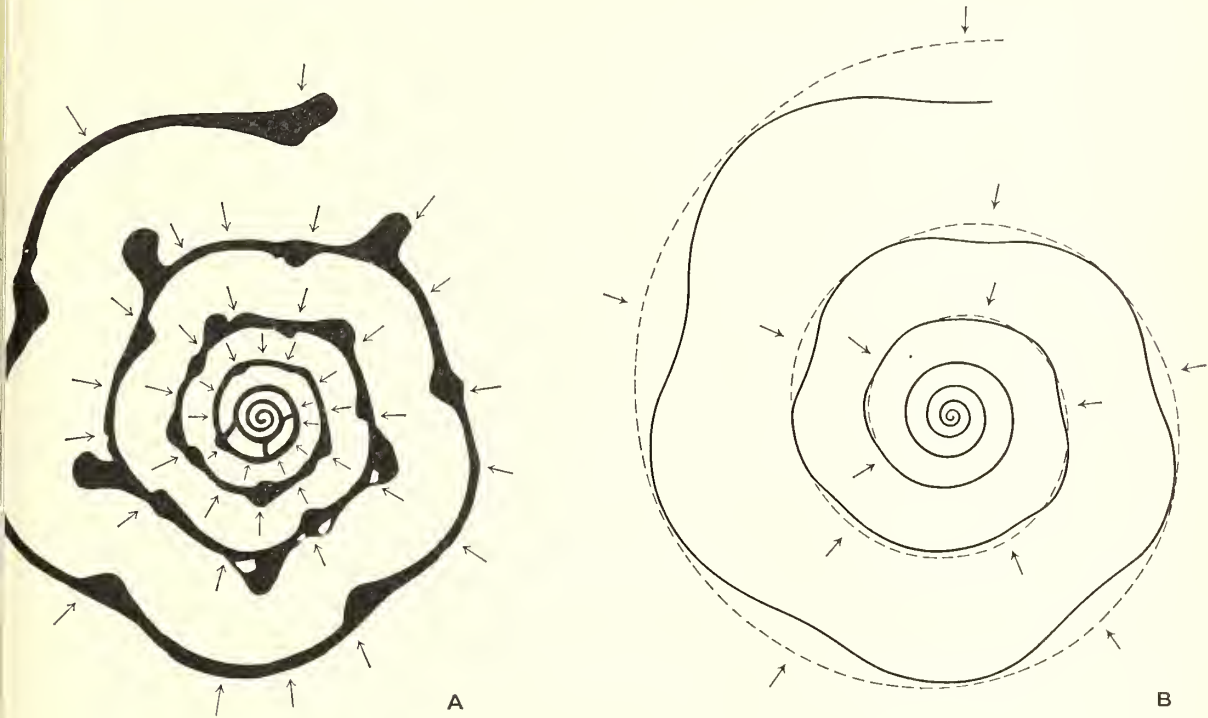
GROWTH

In smooth shells no clearly marked interruptions in growth can be read from the density of the growth-lines. Therefore, the formation of the shell must have been more or less continuous. The same applies to shells with simple ribs, but those with parabolic ribs grew discontinuously, as previously discussed (p. 555). Similarly the regular inner varices following one another at intervals of 69° to 75° (mean 71.5°) in *D. (P.) reussii*, indicate periodic phases of shell deposition between long pauses (text-fig. 5).



TEXT-FIG. 5. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnnes), Ga 1347/56, longitudinal section, $\times 6.3$.

These two growth-rhythms, expressed in the one case by parabolic ribs and in the other by inner varices, occur together and interfere with one another in *D. (P.) angusta*. As in *D. (P.) reussii* the inner varices exhibit pentagonal symmetry (means of 70.4° , 70.7° , and 76° in three measured specimens), and between them three (on inner whorls sometimes two) parabolic ribs are intercalated. These ribs tend to arrange themselves in groups of three towards the last whorl. In this way the first formed parabolic rib of such a group coincides with an inner varix (text-figs. 6A, 7). (The outer varices, seen externally, cannot be exactly transferred into the longitudinal section; their position may therefore be slightly different.)



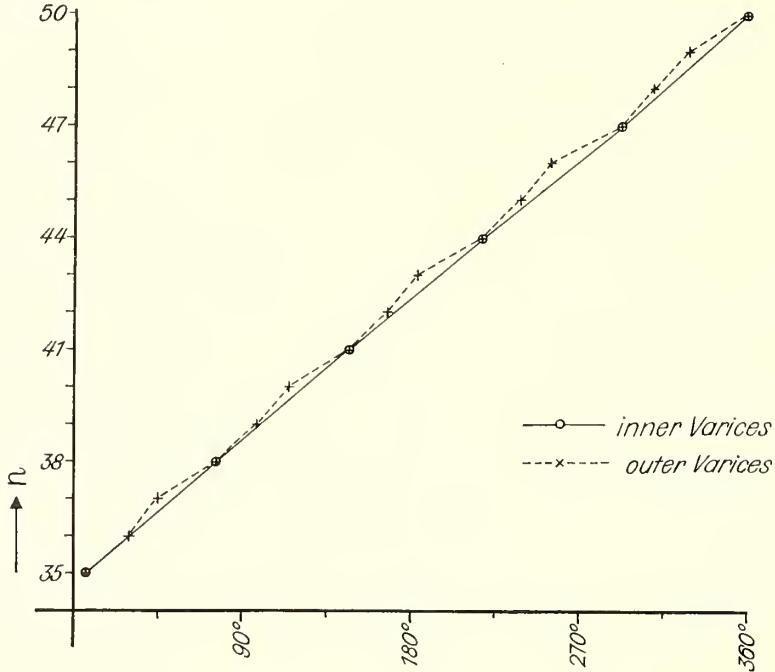
TEXT-FIG. 6. *Discohelix (Pentagonodiscus) angusta* n. sp. A. Ga 1347/53, longitudinal section, $\times 6.3$ (arrows indicate outer varices). B. Ga 1347/51, extrapolation of the normal logarithmic spiral (hatched line) from the regularly coiled inner whorls in comparison to the actual spiral (unbroken line), $\times 6$.

Thus if one considers the parabolic features as brief discontinuities and the inner varices as drawn out breaks in shell secretion, then *D. (P.) angusta* shows complicated double-phased growth, the control of which is unknown.

The subgenus *Pentagonodiscus* assumes a pentagonal outline in the last $2-2\frac{1}{2}$ whorls. In text-fig. 6B the normal logarithmic spiral of the regularly coiled inner whorls has been extrapolated omitting the various irregularities of the shell (inner varices, ribs). This clearly shows that the aberrant shell form commences with the first inner varix and becomes more accentuated as the varices increase in strength towards the aperture. The most prominent deviations from a logarithmic spiral occur at the points of periodic

constrictions of the former peristomes. In the intervening growth-phases the spiral is again followed and thus shows itself to maintain control of the pentagonal coiling.

Among the gastropods, there appear to be only two cases of angular instead of regular spiral coiling: *Triangularia paradoxa* Frech and *Tremanotus polygonus* Barrande. The first has a triangular, and the latter a pentagonal outline. Nothing is known of the internal structure of either of these two species. Periodically constricted apertures were probably also formed and might be revealed by inner varices.



TEXT-FIG. 7. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp. Ga 1347/53. Diagrammatic view of the intervals of the inner and outer varices on the last whorl (n = no. of outer varices, counted from the centre).

Deviations from a logarithmic spiral are widely distributed among ammonoids, but commonly affect only the last body chamber. Triangular coiling in early ontogenetic stages, producing an extremely aberrant shell form, is found solely in a few clymenids (*Solicleymenia*, *Wocklumeria*, *Parawocklumeria*) and goniatites (*Paralegoceras*) (see Schindewolf 1937, p. 110 et seq.). It is conceivable that periodic narrowing of the aperture was also responsible. Deep constrictions, signifying a former aperture at the points of strongest deviation from the normal spiral, occur in two of these genera (*Wocklumeria*, *Parawocklumeria*) and support this supposition. A narrowed body chamber in early ontogenetic stages, remaining unresorbed, and periodicity in growth lead automatically to an angular instead of a spiral shell form. If one imagines further shell growth after the last known peristome of e.g. *Oecoptychius refractus* (Reinecke), an angular outline must necessarily be the result. Not to be confused with such genuine

angular forms are those in which the umbilicus has a polygonal outline as a result of deep constrictions (e.g. *Morphoceras*, some perisphinctids). In longitudinal section they have a perfectly regular logarithmic spiral.

No attempt has been made here to fully explain the phenomenon of triangular ammonoids. The control of such aberrant growth remains as speculative as in polygonally coiled gastropods.

MODE OF LIFE

The planispiral coiling of many *Discohelix* species is reminiscent of ammonoids and suggests adaption to a nektonic mode of life. Thus Koken (1897, p. 42) proposed that the Upper Triassic *Kokenella* (Pleurotomariacea), which is first coiled in a trochospiral and later in a planispiral, was adapted to a free swimming in deep sea. However, no recent gastropod with an almost symmetrical shell is known to be capable of active swimming. A single exception are the pelagic Heteropoda (e.g. *Atlautia*) with a weakly calcified, very thin or wholly vestigial shell. They cannot be compared with the thick-shelled, often strongly sculptured *Discohelix*, for which only a benthonic mode of life can be considered. If the planispiral coiling were an adaption to a nektonic mode of life, then this feature would normally tend to be realized as a result of selection. It turns out, however, to be extremely variable, not only on the specific but also on the generic level.

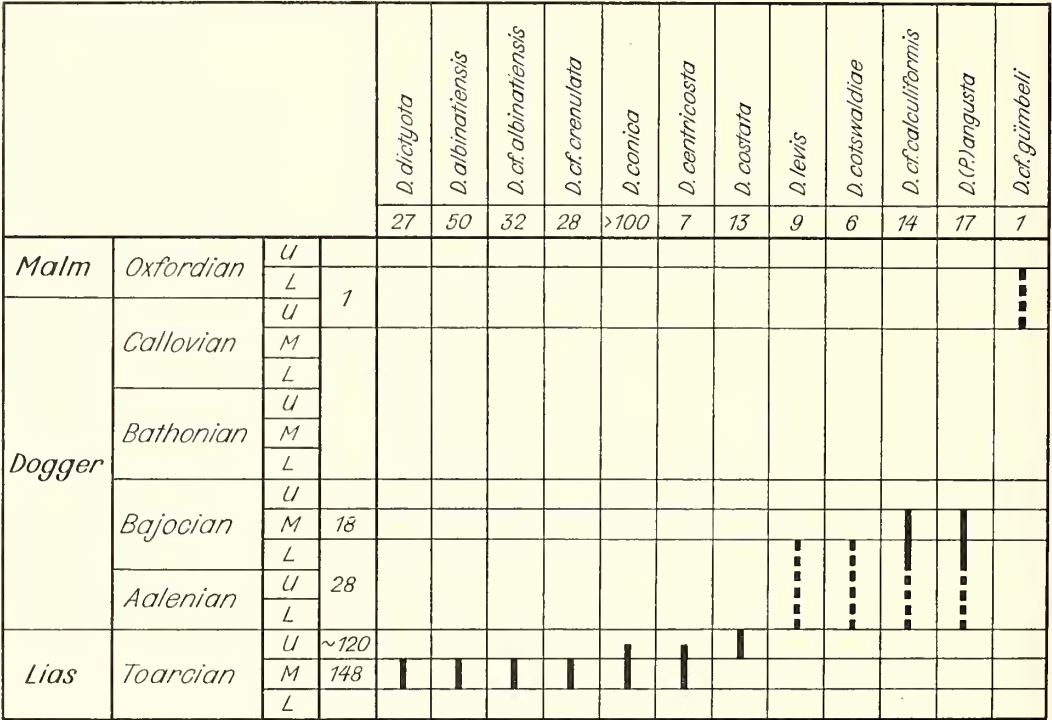
The disc shape, in fact, would appear to be a disadvantage since it is much more susceptible to water movement than a helicocone. This can scarcely have been compensated for by the narrow whorls and the small aperture, indicating a correspondingly small and weak foot. For this reason the most favourable environment for *Discohelix* may have been in quiet sublittoral water or in the shelter of reefs rather than in a disturbed littoral. In a vertical position the pentagonal form can be seen to have an advantage over the spiral form, since the angularity provides a kind of resting surface (cf. *Murex*) allowing the animal a greater stability on the sea-floor. The efficiency of this is increased through the support of lateral spines in *D. (P.) angusta*.

DEVELOPMENT AND VALUE AS INDEX FOSSILS

There are still great gaps in our knowledge of the development of the Euomphalidae in the Triassic. For this reason the exact origin of the genus *Discohelix* has not yet been elucidated. Several Triassic forms described as *Euomphalus* belong to *Woehrmannia*, but the majority are insufficiently known for an exact generic determination.

Typical biconcave shells with more or less bilaterally symmetrical whorls and upper and lower keel appear for the first time in the lowermost Liassic. A greater variety of forms are known from the Sinemurian, especially from the Northern Calcareous Alps (Hierlatz-facies), amongst which are some with a plano-concave cross-section. The transition from biconcave to convexo-concave shells probably occurred several times independently, as has been observed in *D. albinatiensis* (p. 558). A special off-shoot of pentagonally coiled forms (subgenus *Pentagonodiscus*) also commenced in the Sinemurian but with only two stratigraphically isolated species, it has not yet been fully verified. The observed variation of individual features reduces their phylogenetic value and makes it necessary to separate species according to character combinations. Despite

the approximately forty known (many insufficiently) *Discohelix* species their lines of evolution can only be traced at a few points. Their stratigraphical distribution has not been proved because of their sparsity, occurrence as fissure-faunas, and the failure of accompanying index fossils. Therefore the well dated material presented here assumes a special stratigraphical value. From text-fig. 8 it can be seen that the species have only a very short range, extending through only one or a few zones. Similar conclusions can be drawn from the stratigraphical information given by Hudleston (1892, pp. 315–21) for the English Middle Jurassic.



TEXT-FIG. 8. The stratigraphical distribution of *Discohelix* in the condensed Jurassic of Rocca Busambra (Western Sicily); numbers indicate number of specimens.

The strong condensation in the sections made it necessary to use substages instead of zones for the time-scale in text-fig. 8. In three cases the boundaries of the substages could not be drawn since up to five zones are inseparably concentrated in one stratigraphical unit (Wendt 1965, p. 300). For this reason the exact range of some of the species cannot be given. The representatives of *Discohelix* which begin the fossil record in the Middle Toarcian (Bifrons Zone) may have originated earlier. The absence of species from the base of the Bathonian to the Upper Callovian is owing to a stratigraphic gap characteristic of the west Sicilian Jurassic. A diminution of the *Discohelix* fauna is already evident earlier, and the last representative on the Dogger–Malm boundary is almost coincident with the extinction of the genus in the Lower Oxfordian.

It should not be overlooked that the stratigraphical range of the species investigated here is based on a series of sections from a single locality. To date it has been verified in two cases by specimens from the Northern Calcareous Alps. Furthermore well-dated material of *Discohelix* is wanted to complete and, if necessary, correct the ranges of the various species.

SYSTEMATIC DESCRIPTIONS

Only two imperfectly preserved examples were available to Dunker when he established the genus *Discohelix* in 1847, so that even he himself was uncertain of its individuality five years later (see footnote in Reuss 1852, p. 116). Rich material allowed Stoliczka (1861, p. 180 et seq.) to distinguish *Discohelix* from *Euomphalus* and to define it precisely for the first time. Without altering this concept of the genus Cossmann (1915, p. 133 et seq.) included in it both Triassic and Cretaceous species, although they did not completely pass within his diagnosis. In the same publication he proposed the genus *Colpomphalus* (1915, p. 136) for forms with a convex spire transitional to *Discohelix*. This gradation is in fact so continuous, even in one and the same species (see p. 558), that *Colpomphalus* can no longer be maintained as an independent unit. Among the Triassic predecessors of *Discohelix*, *Amphitoniaria* Koken differs through its prosocyrty growth-lines on the outer side, and *Anisostoma* Koken through its peculiar, deflected peristome. (Specimens placed in the latter genus, from which the aperture has been broken, could, in fact, be early members of *Discohelix*.)

Genus *DISCOHELIX* Dunker 1847

Type species. D. caleniformis Dunker 1847.

Diagnosis. Widely to extremely widely umbilicate representatives of the Euomphalidae, with numerous, not overlapping whorls of trapezoidal cross-section, with an upper and lower keel. Mostly dextral, rarely sinistral. Spire concave, plane or convex. Protoconch homeostrophic, not sharply separated from the teleoconch. Growth-lines on the upper and lower sides prosocline, on the outer side opistocyrty. Ornament collabral and/or spiral. Peristome more or less tangential to foregoing whorl, its outline parallel to the axis of coiling, simple or with thickened outer and/or inner lip. Operculum unknown.

Distribution. Triassic? Jurassic (Hettangian to Oxfordian).

Synonym. *Colpomphalus* Cossmann 1915.

Discohelix (*Discohelix*) *dictyota* n. sp.

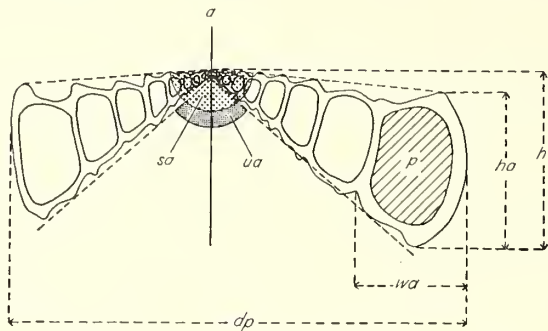
Plate 107, figs. 1-8; text-figs. 2A, 3E

Derivation of name. *dictyotus* = retiform.

Holotype. Ga 1347/1. Plate 107, figs. 1-4.

No.	<i>dp</i>	<i>d</i>	<i>h/d</i>	<i>ha/wa</i>	<i>nw</i>	<i>nt</i>	<i>sa</i>	<i>ua</i>
Ga 1347/1		20.0	0.29	1.49	9	34		
Ga 1347/2	18.3		0.28	1.33	8	(30)	214°	145°
Ga 1347/3		16.4	0.29	1.78	8	33		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, teleoconch with retiform sculpture; peristome unthickened.



TEXT-FIG. 9. Shell measurements. a = axis of coiling, dp = maximum diameter measured at peristome (in mm.), h = height of shell, ha = height of aperture, p = cross-section through peristome (hatched), sa = mean spiral angle, ua = mean umbilical angle, wa = width of aperture.

Additional abbreviations in the measurement-tables: d = diameter (in mm.), nt = number of tubercles (nodes), numbers in () referring to half whorls, nw = number of whorls.

Description. Fine ribs appear after the protoconch contemporaneously with the onset of clear growth-lines. They develop on the keel as nodes, and with good preservation may be recognized on the last whorls as a parabolic feature. On this last whorl the spiral lines, 7–10 on the upper and lower sides and 16–20 on the outer side, are strongest; they fail on the inner whorls of the teleoconch. The final peristome shows no special structure. Before it, on two specimens, a short pause in growth is indicated by a gentle angulation in the shell outline.

Discussion. *D. reticulata* Stoliczka shows a similar sculpture, the spiral lines being restricted to the outer side, however, the whorls are more compressed, and broader than high in cross-section. *D. orbis* (Reuss) can be distinguished by its much finer ornament and clearly differentiated keel, and *D. dunkeri* Moore by its fewer nodes and plano-concave cross-section.

Distribution. Middle Toarcian (Bifrons Zone).

Discohelix (Discohelix) albinatiensis Dumortier 1874

Plate 107, figs. 9–15; Plate 108, figs. 8–10; text-figs. 2B, 3A–B

1874 *Discohelix Albinatiensis* Dumortier, p. 284, pl. 59, figs. 3–5.

? 1892 *Straparollus pulchrior* Hudleston, p. 318, pl. 25, fig. 9.

EXPLANATION OF PLATE 107

Figs. 1–4. *Discohelix (D.) dictyota* n. sp., holotype, Ga 1347/1, $\times 2$.

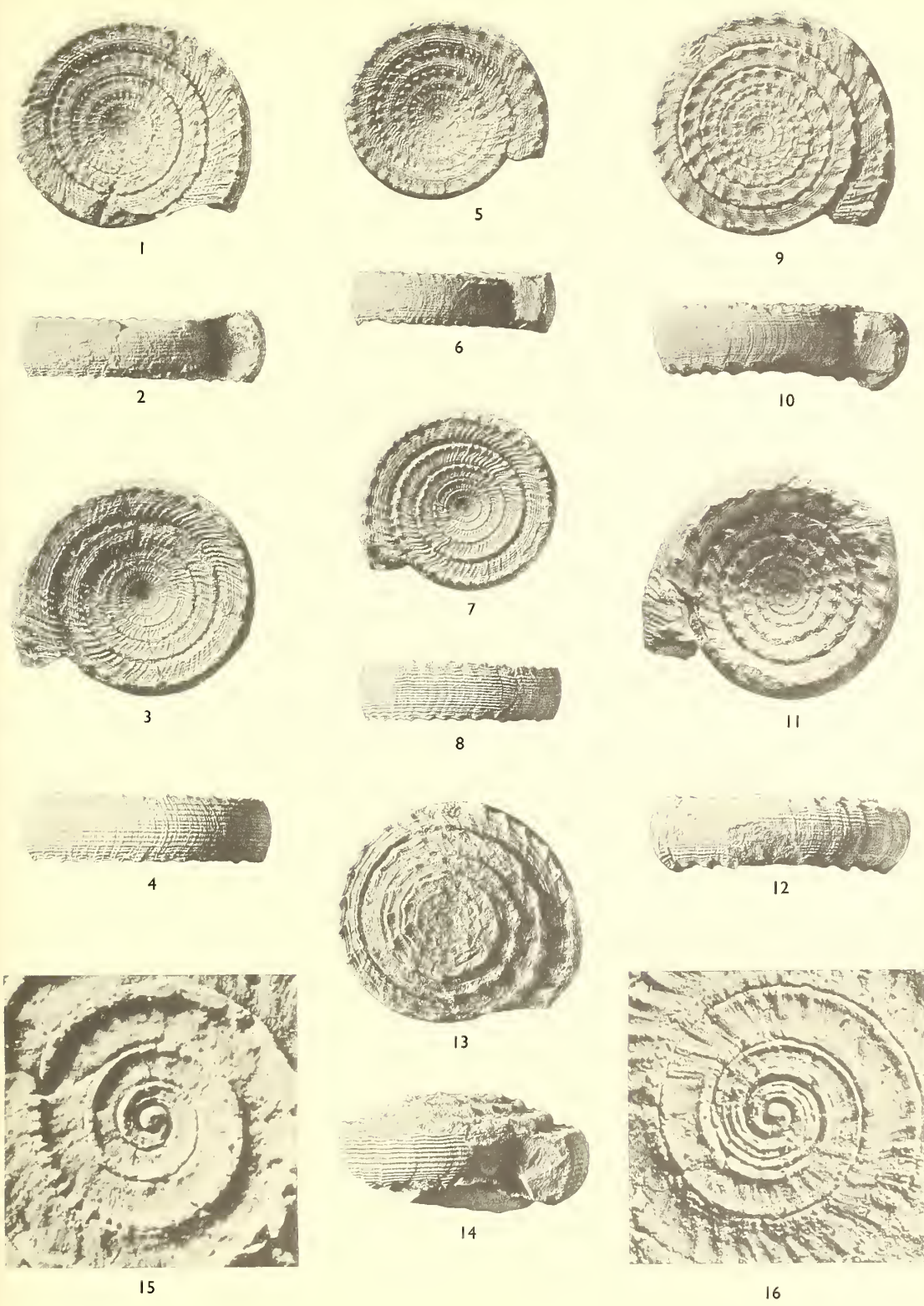
Figs. 5–8. *Discohelix (D.) dictyota* n. sp., Ga 1347/3, $\times 2$.

Figs. 9–12. *Discohelix (D.) albinatiensis* Dumortier, Ga 1347/6, $\times 3$.

Figs. 13–14. *Discohelix (D.) albinatiensis* Dumortier, Ga 1347/8, $\times 3$.

Fig. 15. *Discohelix (D.) albinatiensis* Dumortier, Ga 1347/11. Inner whorls with protoconch, $\times 20$.

Fig. 16. *Discohelix (D.)* cf. *albinatiensis* Dumortier, Ga 1347/14. Inner whorls with protoconch, $\times 20$.



WENDT, *Discohelix* from the Tethyan Jurassic

Lectotype (here selected). Dumortier 1874, pl. 59, figs. 4–5.

No.	dp	d	h/d	ha/wa	nw	nt	sa	ua
Ga 1347/5	15.3		0.29	1.55	8	(16)	184°	120°
Ga 1347/6	14.2		0.32	1.43	8	27		
Ga 1347/7	14.2		0.30	1.48	8	(13)	188°	117°
Ga 1347/8		13.2	0.42	1.22	8	25		
Ga 1347/9		14.4	0.48	1.47	9	(18)	132°	81°
Ga 1347/10		12.4	0.33	1.63	8	12		

Diagnosis. Dextral, spire weakly concave, plane, or weakly convex; protoconch smooth, retiform sculpture on teleoconch; peristome thickened.

Description. The majority of the available specimens are plano-concave, several specimens, however, have a slightly concave or a more or less strongly convex spire. The larval whorls are free of sculpture, with an angulation near the suture, slightly concave upper side, and a smooth keel. The ornament of the teleoconch, beginning after 1½–2 whorls, is similar to, but somewhat coarser than in *D. dictyota*. 20–27 parabolic nodes may be counted on the keel. 10–20% fewer nodes are present on the lower keel, thus emphasizing the asymmetry of the shell. Seven examples varying in diameter between 7 and 13 mm. stand apart from the remainder of the material in that the nodes are more widely spaced (12–15 instead of 20–23 on typical individuals, see Pl. 108, figs. 8–10). A clear spiral ornament begins only after a diameter of 10 mm. has been reached. It may completely fail on the upper and lower sides and be restricted to a small area adjacent to the keel on the outer side. The peristome is internally thickened and therefore narrowed.

Discussion. The larval whorls and peristome were not preserved in the material used by the authors cited in the synonymy, so that the present specimens can only be named with some reservation. Those with the most raised spire cannot be distinguished in cross-section and sculpture of the teleoconch from *D. exsertus* (Hudleston 1892, p. 320, pl. 26, figs. 3–4).

Distribution. Middle Toarcian (Bifrons Zone). The type was thought by Dumortier to have come from the Opalinum Zone, but was found in a loose block of uncertain stratigraphic origin. According to Hudleston (1892, p. 319) *D. pulchrior* occurs rarely in the Murchisonae Zone.

Discohelix (Discohelix) cf. albinatiensis Dumortier 1874

Plate 107, fig. 16; Plate 108, figs. 1–7; text-figs. 1A, 3D

? 1935 *Discohelix albinatiensis* Dumortier; Roman, p. 32, pl. 6, figs. 1, 1a.

No.	dp	d	h/d	ha/wa	nw	nt	sa	ua
Ga 1347/13	22.9		0.37	1.40	9	29		
Ga 1347/14		21.0	0.41	1.96	9	30		
Ga 1347/15	19.4		0.39	1.52	9	(16)	171°	99°
Ga 1347/16		16.3	0.47	1.73	8	(14)	165°	90°

Description. In contrast to typical members of the species spiral sculpture is totally lacking on the last whorls, but 2–3 spiral lines may be traced on the upper side of the

protoconch. From these two characters a decisive separation from *D. albinatiensis* is not possible.

Distribution. Middle Toarcian (Bifrons Zone).

Discohelix (Discohelix) cf. crenulata (Moore 1867)

Plate 108, figs. 11–16; text-figs. 3F, G

cf. 1867 *Solarium crenulatum* Moore, p. 90, pl. 4, figs. 19–20.

No.	dp	d	h/d	la/wa	nw	nt	sa	ua
Ga 1347/19	14.4		0.46	1.41	9	(30)	148°	87°
Ga 1347/20		13.3	0.38	1.42	8	50		
Ga 1347/21		12.8	0.52	1.50		54		
Ga 1347/23	7.7		0.57	1.36	7		147°	76°

Description. The shell form of this dextrally coiled species varies from almost plano-concave ($sa = c. 170^\circ$) to clearly convexo-concave. The mean umbilical angle varies correspondingly between relatively wide boundaries. The protoconch has distinct spiral lines, and after $1\frac{1}{2}$ –2 whorls fine ribs appear which rise to small nodes on the keel. Later, spiral lines reappear so that the sculpture is similar to that of *D. dictyota* and *D. dum-driensis* (Tawney), as Hudleston (1892, pl. 26, fig. 2) figured in detail. However, the external spiral lines are seldom regularly distributed over the whole outer side of the last whorl, and a smooth band is left free in the centre.

In the available material two varieties differing in their whorl number can be distinguished: one having 7 whorls at a maximum of approximately 8 mm. in diameter, and the other 8–9 whorls at 13–15 mm. in diameter. The aperture of the small examples is thickened (text-fig. 3G) and that one of the large ones is simple and unthickened (text-fig. 3F).

Discussion. Moore's figure and description do not give a clear impression of this species and it has not since been mentioned. Therefore no comparison of the shell cross-sections can be made, but aside from this the present specimens have a much wider umbilicus. A similar umbilicus is possessed by *D. crussoliensis* Roman (1935, p. 102, pl. 3, figs. 5, 5a), but this species is considerably more conical. *D. helenae* (Dumortier 1874, p. 141, pl. 36, figs. 1–4) has a comparable shell shape but the nodes on the keels are coarser and more widely spaced (18 in contrast to 50–60 in *D. cf. crenulata*).

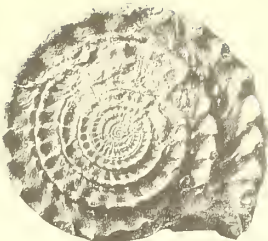
Distribution. Middle Toarcian (Bifrons Zone). The type was said to be from the upper Middle Liassic.

EXPLANATION OF PLATE 108

- Figs. 1–2. *Discohelix (D.) cf. albinatiensis* Dumortier, Ga 1347/13, $\times 2$.
 Figs. 3–4. *Discohelix (D.) cf. albinatiensis* Dumortier, Ga 1347/18, $\times 2$.
 Figs. 5–7. *Discohelix (D.) cf. albinatiensis* Dumortier, Ga 1347/17, $\times 2$.
 Figs. 8–10. *Discohelix (D.) albinatiensis* Dumortier, Ga 1347/10, $\times 3$.
 Figs. 11–13. *Discohelix (D.) cf. crenulata* (Moore), Ga 1347/21, $\times 3$.
 Figs. 14–16. *Discohelix (D.) cf. crenulata* (Moore), Ga 1347/22, $\times 3$.
 Figs. 17–21. *Discohelix (D.) conica* n. sp., holotype, Ga 1347/25, $\times 3$.
 Fig. 21. *Discohelix (D.) conica* n. sp., Ga 1347/27, $\times 3$.



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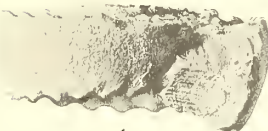
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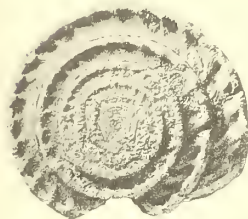
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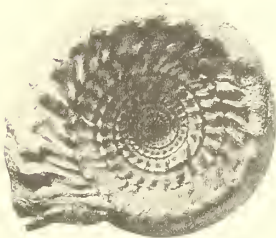
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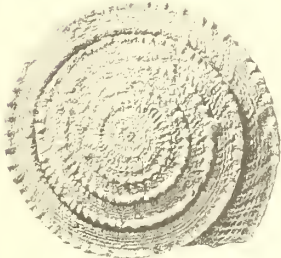
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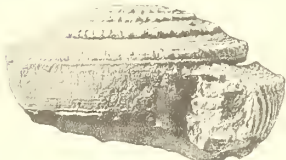
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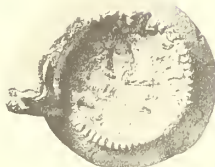
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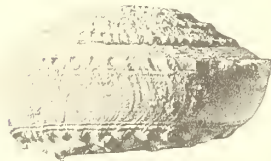
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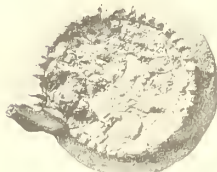
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Discohelix (Discohelix) conica n. sp.

Plate 108, figs. 17–21; text-figs. 2C–D, 3C

Holotype. Ga 1347/25. Plate 108, figs. 17–20.

No.	<i>dp</i>	<i>h/d</i>	<i>ha/wa</i>	<i>nw</i>	<i>sa</i>	<i>ua</i>
Ga 1347/24	9.1	0.64	1.52	7	124°	63°
Ga 1347/25	9.3	0.65	1.42	7		
Ga 1347/26	10.7	0.53	1.31	7½	132°	74°

Diagnosis. Small, dextral, spire convex; protoconch spirally ornamented, on teleoconch only growth-lines, smooth upper and finely tuberculated lower keel; peristome thickened.

Description. Three spiral lines can be traced on the depressed protoconch and disappear after 1–1½ whorls. From approximately the fourth whorl fine nodes appear close to the suture, stretched out in the direction of the growth-lines but not reaching the smooth upper keel. The lower keel is formed by a succession of fine tubercles which are accompanied on the outer side by 2–3 undulating spiral lines. The externally thickened peristome can sometimes be seen to have been preceded on the last whorl by 1–2 growth interruptions (text-figs. 2C–D).

Discussion. *D. conica* contrasts with the above species in having a higher spire. Furthermore the failure of spiral ornament and the smooth upper keel are good specific characters.

Distribution. Middle to lower Upper Toarcian (Bifrons to c. Thouarsense Zone).

Discohelix (Discohelix) centricostan n. sp.

Plate 109, figs. 1–7; text-fig. 3I

Holotype. Ga 1347/30. Plate 109, figs. 1–3.

No.	<i>dp</i>	<i>d</i>	<i>h/d</i>	<i>ha/wa</i>	<i>nw</i>	<i>sa</i>	<i>ua</i>
Ga 1347/30		23.0	0.31	1.51	8		
Ga 1347/31	25.6		0.35	1.29	9	217°	136°
Ga 1347/32	18.4		0.32	1.75	8		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, nepionic whorls ribbed, neanic whorls smooth; peristome trumpet-like.

Description. The shell consists of 7–9 whorls and the spire is almost as depressed as the umbilicus resulting in a nearly symmetrical cross-section. The 2–4 whorls following the spirally ornamented protoconch have weak ribs and finely tuberculate keels. These elements become less accentuated with growth. The last whorls are completely smooth or show only traces of a slight undulation. The aperture, which is only preserved in two cases, is broadened and thickened to an almost circular cross-section in the larger specimen (text-fig. 3I), and in the smaller (Ga 1347/32) is similar in cross-section to the preceding whorls.

Discussion. Without knowledge of the protoconch this species cannot be separated from *D. calculiformis* Dunker.

Distribution. Middle to lower Upper Toarcian (Bifrons to c. Thouarsense Zone).

Discohelix (Discohelix) costata n. sp.

Plate 109, figs. 12–18; text-fig. 3K

Holotype. Ga 1347/34. Pl. 3, figs. 15–18.

No.	dp	d	h/d	ha/wa	nw	nt	sa	ua
Ga 1347/34		24.8	0.42	1.83	9	29		
Ga 1347/35	25.0		0.38	1.46	8	(13)	213°	129°
Ga 1347/36	19.8		0.32	1.42	8	27		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, teleoconch ribbed; peristome thickened, somewhat broadened.

Description. 4–5 spiral lines are present on the upper and lower side of the protoconch, but are quite absent from the following whorls. They are ornamented by regular ribs which may be traceable in the nepionic stage or only on the last whorl. The outer side, between the strongly corrugated keels, is completely smooth except for fine growth-lines.

Discussion. The biconcave shell form, the failure of spiral lines, and the strong sculpture make *D. costata* a very distinctive species. A phylogenetic connection with *D. centricosta* seems probable, *D. costata* having originated from this species through a persistence of the ribbing to the last whorl.

Distribution. Upper Toarcian (c. Variabilis to Levesquei Zone).

Discohelix (Discohelix) levis n. sp.

Plate 109, figs. 8–11; text-figs. 2E, 3L

Derivation of name. *levis* = smooth.

Holotype. Ga 1347/38. Plate 109, figs. 8–9.

No.	dp	d	h/d	ha/wa	nw	sa	ua
Ga 1347/37	22.7		0.38	1.29	8	211°	124°
Ga 1347/38	19.7		0.36	1.51	8		
Ga 1347/39	15.6		0.33	1.30			
Ga 1347/40		19.8	0.37	1.59	8		

EXPLANATION OF PLATE 109

Figs. 1–3. *Discohelix (D.) centricosta* n. sp., holotype, Ga 1347/30, $\times 2$.

Figs. 4–6. *Discohelix (D.) centricosta* n. sp., Ga 1347/32, $\times 2$.

Fig. 7. *Discohelix (D.) centricosta*, n. sp., Ga 1347/33, $\times 3$.

Figs. 8–9. *Discohelix (D.) levis* n. sp., holotype, Ga 1347/38, $\times 2$.

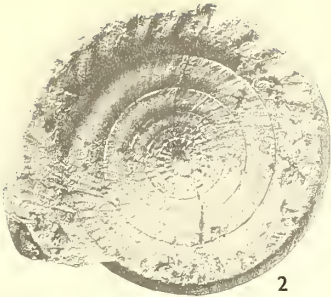
Figs. 10–11. *Discohelix (D.) levis* n. sp., Ga 1347/40, $\times 2$.

Figs. 12–14. *Discohelix (D.) costata* n. sp., Ga 1347/36, $\times 2$.

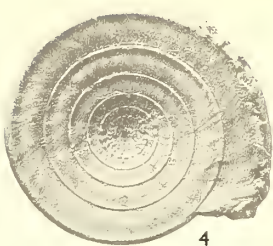
Figs. 15–18. *Discohelix (D.) costata* n. sp., holotype, Ga 1347/34, $\times 2$.



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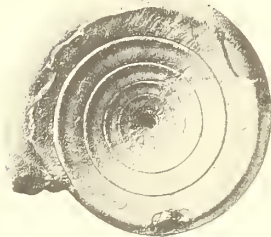
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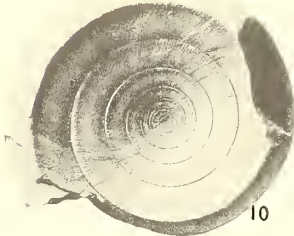
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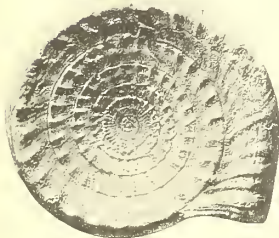
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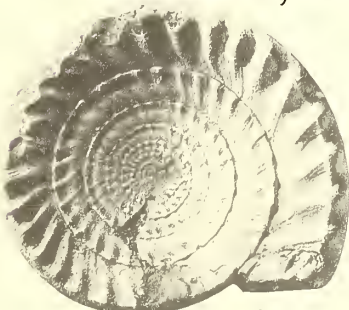
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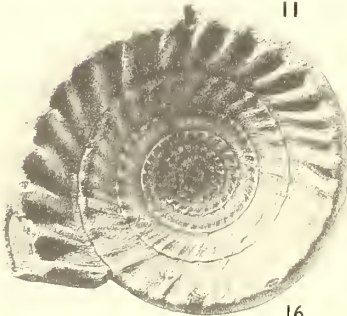
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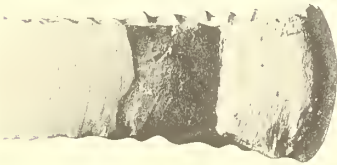
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18

WENDT, *Discohelix* from the Tethyan Jurassic

Diagnosis. Dextral, spire concave; protoconch and teleoconch smooth; peristome broadened and thickened.

Description. The smooth shell is only ornamented with growth-lines, which become stronger towards the keel causing it to be corrugated. The slight asymmetry of the cross-section is seen in the greater depression of the umbilicus relative to the spire, and in the irregular curvature of the outer side. In three specimens the trumpet-like aperture is preserved and is reinforced by an inner varix on the outer lip.

Discussion. The shape is very similar to *D. excavata* (Reuss) without being as high as this species ($h/d = 0.43-0.48$ in Stoliczka's originals). Apart from this the keel in *D. levis* remains smooth as far as the peristome, whilst in *D. excavata* more or less strong nodes appear on the last half-whorl. The sculpture of the protoconch of this last species is unknown.

Distribution. Aalenian to Lower Bajocian (condensed Opalinum to Sauzei Zone).

Discohelix (*Discohelix*) cf. *calculiformis* Dunker 1847

Plate 110, figs. 1-4; text-fig. 3H

cf. 1884 *Discohelix calculiformis* Dunker; Quenstedt, p. 325, pl. 197, figs. 32, 33, 35.

No.	<i>dp</i>	<i>d</i>	<i>h/d</i>	<i>ha/wa</i>	<i>nw</i>	<i>sa</i>	<i>ua</i>
Ga 1347/42		16.1	0.36	1.80	8	213°	135°
Ga 1347/43		20.4	0.31	1.66	8		
Ga 1347/44	21.1		0.36	1.48	8		
		18.6	0.34	1.64			

Description. The umbilicus is somewhat more depressed than the spire and only this reveals the dextral coiling of the species. The cross-section of the whorls is regularly trapezoidal. The sculpture of the protoconch, consisting of 5-6 spiral lines on the first two whorls, is clearly different from that of the teleoconch. The following whorls are ornamented as in *D. levis* but the keel is more sharply expressed and the outer side less strongly curved. The aperture, preserved in only one specimen, is somewhat broadened and thickened on the outer side.

Discussion. *D. calculiformis* Dunker, founded on two badly preserved specimens and an unsatisfactory figure, was regarded by its author five years later as probably identical with *D. orbis* (Reuss 1852, p. 116). On the one hand Quenstedt's originals of *D. calculiformis* and on the other hand Stoliczka's of *D. orbis* (1861, p. 182, pl. 3, figs. 8-10), as well as other topotypic material of the last species are available to me for comparison. The first seem to have a smooth protoconch and no trace of spiral ornament on the later whorls; the last show a very fine spiral sculpture which can also be seen in Stoliczka's figures. The present specimens differ from both these species in the spiral ornament on the protoconch and the smooth teleoconch. They have here been attached with open nomenclature to *D. calculiformis* sensu Quenstedt, from which they cannot be confidently

separated without knowledge of the protoconch. The erection of a new species does not seem to be justified so long as *D. calculiformis* remains so poorly known.

Distribution. Aalenian to Middle Bajocian (condensed Opalinum to c. Subfurcatum Zone).

Discohelix (Discohelix) cotswoldiae (Lycett 1850)

Plate 110, figs. 5–12; text-figs. 2F, 3M

1850 *Solarium Cotswoldiae* Lycett, p. 419, pl. 11, figs. 2, 2a.

1892 *Discohelix Cotswoldiae* Lycett; Hudleston, p. 316, pl. 25, fig. 7.

No.	dp	d	h/d	ha/wa	uw	sa	ua
Ga 1347/45		12.0	0.31	1.84	7	218°	142°
Ga 1347/46	16.2		0.33	1.23	7 $\frac{2}{3}$		
		13.6	0.35	2.40			
Ga 1347/47	14.7		0.32	1.57	7 $\frac{1}{2}$		
		13.7	0.29	1.60			

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, retiform sculpture on teleoconch; peristome broadened with inner varices on inner and outer lips.

Description. The umbilicus of the almost perfectly biconcave shell is commonly somewhat more depressed than the upper side. The slightly raised nucleus indicates that the species is dextral. The fine spiral lines of the protoconch reappear only on the last two whorls, but may sometimes be seen earlier on the keel. The carinae are more or less clearly marked and finely corrugated in the nepionic stage. On the last whorl a fine tuberculation may be developed, as can be seen in Hudleston's figure. However, the keel can remain almost perfectly smooth. Externally the peristome is trumpet-like, and internally thickened by strong varices on the inner and outer lips.

Discussion. Specimens with smooth keels resemble the inner whorls of *D. orbis* (Reuss), from which they probably cannot be separated without knowledge of the protoconch and peristome: *D. orbis* having apparently a smooth protoconch, and an un- or only slightly broadened peristome which is not narrowed internally. The fine retiform sculpture differentiates the present species from *D. calculiformis*.

Distribution. Aalenian to Lower Bajocian (condensed Opalinum to Sauzei Zone).

EXPLANATION OF PLATE 110

Figs. 1–3. *Discohelix (D.)* cf. *calculiformis* Dunker, Ga 1347/44, $\times 2$.

Fig. 4. *Discohelix (D.)* cf. *calculiformis* Dunker, Ga 1347/43, $\times 2$.

Figs. 5–8. *Discohelix (D.) cotswoldiae* (Lycett), Ga 1347/46, $\times 2$.

Figs. 9–11. *Discohelix (D.) cotswoldiae* (Lycett), Ga 1347/47, $\times 2$.

Fig. 12. *Discohelix (D.) cotswoldiae* (Lycett), Ga 1347/48, $\times 2$.

Figs. 13–16. *Discohelix (D.)* cf. *gümbeli* Ammon, Ga 1347/49, $\times 3$.

Fig. 17. *Discohelix (Pentagonodiscus) angusta* n. sp., Ga 1347/53, $\times 3$.

Figs. 18–21. *Discohelix (Pentagonodiscus) angusta* n. sp., holotype, Ga 1347/50, $\times 2$.

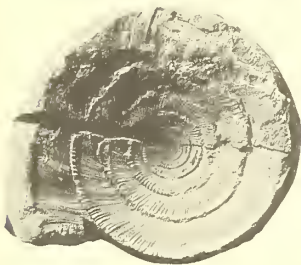
Figs. 22–24. *Discohelix (Pentagonodiscus) reussii* (Hörnes), lectotype, Geol. Bundesanst. Vienna 2980, $\times 2$.



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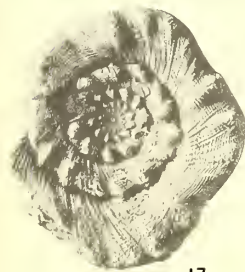
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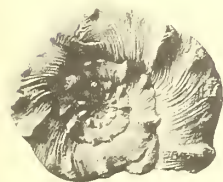
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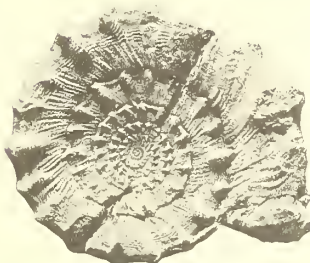
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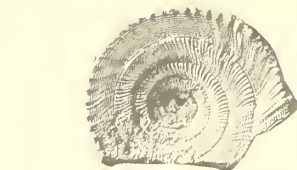
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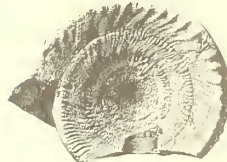
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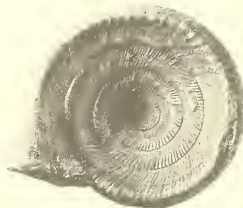
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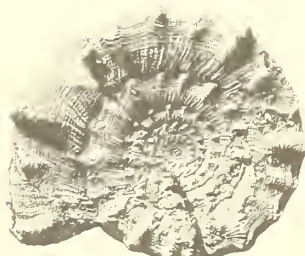
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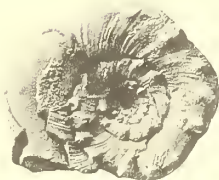
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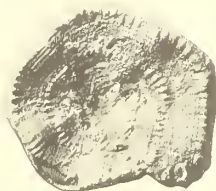
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Discohelix (*Discohelix*) cf. *gümbeli* Ammon 1893

Plate 110, figs. 13–16; text-fig. 3N

cf. 1893 *Discohelix Gümbeli* Ammon, p. 215, text-fig. 39.

No.	dp	h/d	ha/wa	nw	nt	sa	ua
Ga 1347/49	14.0	0.38	1.40	6½	17	222°	142°

Description. That the perfectly biconcave shell is dextral, can only be seen in the somewhat asymmetrical outline of the peristome. The spiral lines of the protoconch disappear after $1\frac{1}{2}$ whorls with the onset of strong ribs which swell to parabolic nodes on the keel. Spiral ornament reappears only on the last two whorls and remains restricted to the keels leaving a smooth band between them on the external side. The peristome, in contrast to the growth-lines, lies almost in a shell radius and has thickened margins.

Discussion. A comparison with the holotype must be restricted to its figure, since the specimen itself, formerly in the Bayer. Staatssammlung Pal. hist. Geol. in Munich, has been lost. From this figure it appears that *D. gümbeli* has higher whorls (*h/d* is said to be 0.5) and a more asymmetrical cross-section. *D. sappho* (Orbigny) is similarly ornamented, but is plano-concave.

Distribution. Upper Callovian/Lower Oxfordian (together with *Distichoceras bicostatum* (Stahl)). The holotype is from the Lias-Dogger boundary.

Discohelix (*Pentagonodiscus*) subgen. nov.

Type species. *D. (P.) angusta* n. sp.

Diagnosis. Subgenus of *Discohelix* in which the last 2–3 whorls are pentagonal in outline owing to periodical deviation of the peristome at intervals of approximately 72°. Inner whorls coiled in a normal logarithmic spiral. Spire concave, dextral. Growth-lines and ornament as in *Discohelix* (*Discohelix*).

Discohelix (*Pentagonodiscus*) *angusta* n. sp.

Plate 110, figs. 17–21; text-figs. 1B, 2H, 3O, 4A–B, 6A–B, 7

Derivation of name. *angustus* = narrow (referring to the peristome).

Holotype. Ga 1347/50. Plate 110, figs. 18–21; text-fig. 1B.

No.	dp	d	h/d	ha/wa	nw	nt	sa	ua
Ga 1347/50	14.6		0.38	1.38	7	12		
Ga 1347/51	12.9		0.33	1.28	6			
Ga 1347/52		12.6	0.37	1.25	6		210°	129°

Diagnosis. Protoconch smooth, retiform sculpture, and parabolic ribs on teleoconch; peristome with inner varices on inner and outer lip.

Description. The sculpture is similar to that of *D. cf. gümbeli*, but much more irregular through the arrangement of the ribs into groups of three. Between the nodes the whorl cross-section is almost round. In contrast *D. (P.) reussii* has broad trapezoidal whorls and is also distinguishable by the failure of ribs. (See also sections 'Parabolic ribs' and 'Growth').

Distribution. Aalenian to Middle Bajocian (condensed Opalinum to c. Subfurcatum Zone).

Discohelix (Pentagonodiscus) reussii (Hörnes 1853)

Plate 110, figs. 22–4; text-figs. 2G, 3P, 5

- 1853 *Euomphalus Reussii* Hörnes; Hauer, p. 760.
 1861 *Discohelix Reussi* Hörnes; Stoliczka, p. 184, pl. 3, figs. 13, 14a–c, non fig. 14d.
 1897 *Discohelix Reussi* Hörnes; Krafft, p. 211.
 1911 *Discohelix Reussi* Hörnes; Gemmellaro, p. 215, pl. 9, fig. 14.
 1935 *Discohelix Reussi* Hörnes, Wähner, p. 22.

Material. Eight specimens, of which five are Stoliczka's originals.

Lectotype. (here selected) Stoliczka 1861, pl. 3, figs. 14a–b (here refigured Pl. 110, figs. 22–4).

No.	<i>d</i>	<i>h/d</i>	<i>lu/wa</i>	<i>nw</i>	<i>sa</i>	<i>ua</i>
2980	14.5	0.43	1.97	6		
Ga 1347/55	15.8	0.42	1.58	6	221°	123°

Diagnosis. Fine retiform sculpture on teleoconch; peristome narrowed with inner varix on outer lip.

Description. Even without a longitudinal section Stoliczka supposed the occurrence of inner varices. The aperture, recurring periodically at mean intervals of 71.5° (Ga 1347/56) is depressed on the outer side and somewhat broadened on the upper and lower sides. This results in regular swellings which are especially strong in the specimen figured by Stoliczka on pl. 3, fig. 13. In the remaining examples the keel has a regularly undulating profile. The peristome is only slightly thickened on its inner lip, but narrowed by a strong inner varix on the outer lip as in *D. (P.) angusta*.

Distribution. Sinemurian–Pliensbachian. According to their label Stoliczka's specimens came from the Oxynotum Zone (Hierlatz) and the Obtusum Zone (Kratzalde). The horizon of Wähner's material is not known; a personal specimen from the same area (Sonnwend Mountains) was found with *Arietites sensu lato*. The examples of Krafft and Gemmellaro are said to be younger (Middle Lias), as is that from the Tübingen Pal. Inst. collection which is the only known extra-alpine occurrence of the species.

CONCLUSION

The stratigraphical division of thick sequences of the Jurassic in the Tethys region is often made extremely difficult by the sparsity or failure of zonal ammonites, and the knowledge of other fossil groups is still insufficient to replace them as stratigraphical indicators. The present investigation of the little-known gastropod genus *Discohelix* may help to fill this gap, since, although this genus is only sporadic in the epicontinental Jurassic, it is occasionally very frequent in the Alpine–Mediterranean area (e.g.

Hochfeln Limestone, Hierlatz Limestone, Liassic Reef Limestone of Sicily). The value of its species as index fossils, shown here, may make possible the division of such cephalopod free or poor series in the Tethyan Lower and Middle Jurassic.

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J. WENDT

Institut für Geologie und Paläontologie
Tübingen, Germany

PEDICELLARIAE OF TWO SILURIAN ECHINOIDS FROM WESTERN ENGLAND

by D. BRYAN BLAKE

ABSTRACT. Pedicellariae have been discovered on the Silurian (Ludlovian) echinoids *Echinocystites pomum* and *Palaeodiscus ferox* from Leintwardine, England. All pedicellariae of both species are tridentate in form and simple in morphology. Most are interambulacral in position. Pedicellariae of *E. pomum* are abundant, all are probably three-valved, and of variable size. Those of *P. ferox* are relatively rare, apparently two-valved, and small in size. These pedicellariae, and an Australian occurrence, are the oldest known echinoid pedicellariae. The unusually large size of one fossil pedicellaria, combined with a general morphology of all pedicellariae intermediate between that of spines and modern pedicellariae suggests that pedicellariae were derived from spines.

WHILE studying materials in the Echinoderm Collections of the British Museum (Natural History), Dr. J. Wyatt Durham observed pedicellariae on specimens of the Silurian echinoid *Echinocystites pomum* and made latex casts of four specimens (three with pedicellariae) of this species and of two specimens of *Palaeodiscus ferox*. In subsequent studies, the writer observed the presence of pedicellariae on both specimens of *P. ferox*. All fossils are from the Ludlow Flags of Leintwardine, Herefordshire. These occurrences, with that of Philip (1963), who recorded pedicellariae associated with a lepidocentroid from rocks regarded as Ludlovian in age from New South Wales, Australia, represent the oldest known echinoid pedicellariae and thus merit detailed consideration.

The Leintwardine material has been studied by many workers including Gregory (1897), Thomson (1861), and Hawkins (1927) but the presence of pedicellariae has not been previously noted in spite of the fact that one of the specimens is the lectotype of *Echinocystites pomum*. Mortensen (1928–51) considered pedicellariae important in echinoid systematics in his monograph of the group but noted and regretted the rarity of fossil pedicellariae (op. cit., vol. 1, p. 33). He did not mention pedicellariae in his discussion of either of these two genera (op. cit., vol. 2, pp. 54–6, 60–3). Reports of the few described Palaeozoic pedicellariae are reviewed by Geis (1936).

Acknowledgements. Dr. Durham made available latex casts of specimens of *E. pomum* and *P. ferox*; the original external moulds of these specimens are in the collections of the British Museum (Natural History) in London. Dr. Porter M. Kier loaned a specimen of *E. pomum* belonging to the Geological Survey of Great Britain which he had prepared for study and identified. Thanks are due to Dr. R. P. S. Jefferies and the authorities of the British Museum (Natural History) for permitting Dr. Durham to prepare latex casts of their specimens and to Dr. Jefferies for information on the histories of some of the specimens.

Echinocystites pomum

All pedicellariae appear to be of the tridentate type, and all probably originally had three valves. ('Tridentate' is one of the four basic types of pedicellariae; most, but not all, have three valves (Mortensen, op. cit., vol. 2, p. 33).) They are numerous; sixty were counted on one incompletely preserved test. The blades of a pedicellaria are in contact

throughout their length; they are slender and elongate with a circular cross-section, and are attenuated distally. The blades bear longitudinal striae but apparently no marginal dentition; their general morphology is essentially identical to that of the spines. The bases are triangular and grade evenly into the blades. Unlike blades of many tridentate pedicellariae, there is little or no constriction near the base. The interior of the base is massive, apparently without a sharp keel-like apophysis. Many heads are located near to tubercles suggesting that stems were lacking, very short, or had contracted upon death. Small pedicellariae are most common, but a considerable range in size exists; there are no distinct size classes. Bases range in diameter from under 0.25 mm. to about 1.75 mm. In general, head length in essentially complete examples ranges from about 0.75 mm. in specimens with small bases to about 3.75 mm. on a specimen of base diameter of 0.75 mm. However, one unusually large pedicellaria (text-fig. 1A) has a base diameter of 1.75 mm. and a length slightly over 11 mm. Blade length is not necessarily directly proportional to base diameter because blade length on bases of a given size is variable.

Only two valves are visible on a number of pedicellariae. However, the great variability of preservation of the three-valved forms and the essential similarity of morphology between those with three valves and those with only two implies that the apparent two-valved pedicellariae are probably incompletely preserved typical three-valved pedicellariae.

With two possible exceptions, all pedicellariae are interambulacral in position. They are widely distributed on the interambulacral columns; on one specimen, pedicellariae occur on plates which border the madreporite, while on another, pedicellariae occur on plates near the peristome. They may be densely grouped, occurring on neighbouring plates, or in some cases, more than one on a single plate. There appears to have been no areal restriction of pedicellariae of certain sizes, for large and small pedicellariae occur on neighbouring plates.

Material examined. Casts of B.M. (N.H.) BMNH 40158; E34352 (lectotype); 40156; GSM 102622.

Palaeodiscus ferox

Pedicellariae are rare on specimens of this species; only two well-preserved pedicellariae have been observed on each of the two specimens. In addition, a number of doubtful pedicellariae are present.

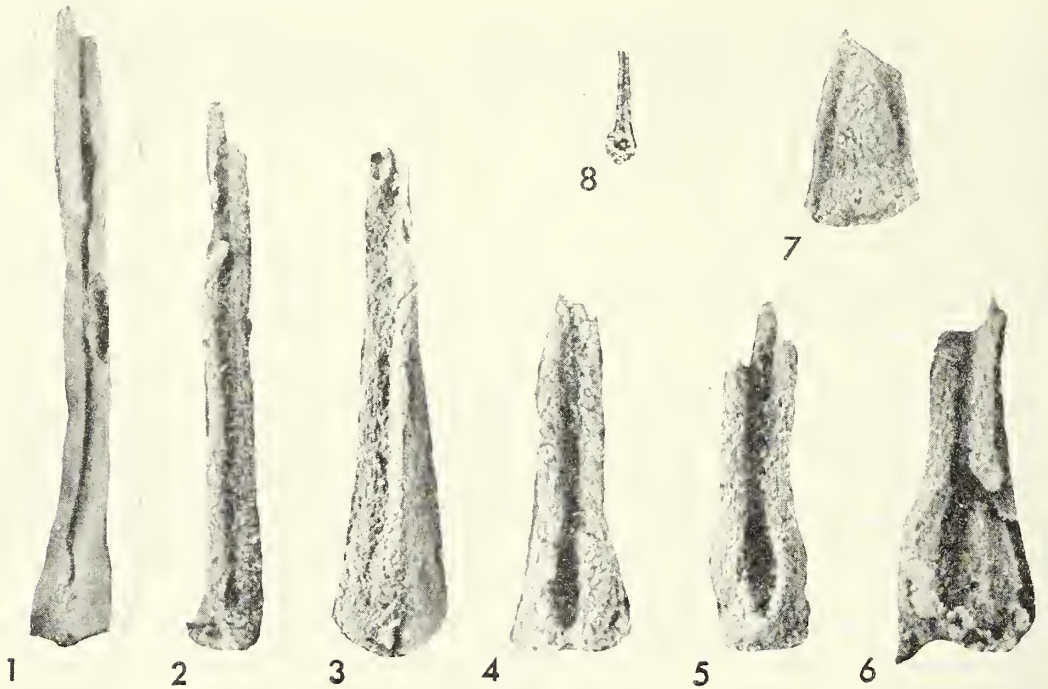
All pedicellariae are tridentate in form but with only two valves; there is no evidence for a third valve. The heads are elongate, triangular, and rounded proximally. The blades, like those of *Echinocystites*, are morphologically very similar to the spines; they are slender, elongate, circular, or sub-circular in cross-section, with longitudinal striae, and in contact throughout their length. There appears to have been no marginal dentition. Bases appear to have been triangular and only slightly enlarged. The heads are very small with a basal dimension of approximately 0.2 mm. and a length of about 0.8 mm. One of the well-preserved pedicellaria is ambulacral in position located near the groove between the rows of ambulacral plates; the others are interambulacral in position.

Although relatively few pedicellariae can be identified, the similarity of morphology between the blades and the spines suggests more pedicellariae may be present but are incompletely preserved or exposed and therefore unrecognized.

Material examined. Casts of *Palaeodiscus ferox*, BMNH E34360 and E34362.

DISCUSSION

The presence of previously unrecorded pedicellariae, in one case abundant, on much-studied echinoid species suggests fossil pedicellariae are probably more common than



TEXT-FIGS. 1A-G. *Echinocystites pomum* pedicellariae. 1, GSM 102622, $\times 7.5$. 2-5, 7, B.M. 40156, $\times 20$. 6, from B.M. E34352, $\times 20$. H. *Palaeodiscus ferox* pedicellaria. B.M. E34360.

previously has been thought. Further, because two families of Silurian echinoids are involved, evolution of these structures must have been relatively early and fairly widespread.

In many features, the Silurian pedicellariae are spine-like. The valves are circular in cross-section, the surface ornamentation is similar to that of the spines, marginal dentition is absent, the base of the blade is not strongly constricted, blades of a pedicellaria are in contact throughout their length, the bases are massive without a sharp apophysis. Further, one unusually long spine-like pedicellaria is present. These features render the Silurian pedicellariae morphologically intermediate between spines and modern types of pedicellariae and suggest the possibility that pedicellariae were derived from spines.

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D. BRYAN BLAKE
Department of Geology
University of Illinois
Urbana, Illinois 61801
U.S.A.

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MACROCYSTELLA CALLAWAY, THE EARLIEST GLYPTOCYSTITID CYSTOID

by C. R. C. PAUL

ABSTRACT. *Macrocystella mariae* Callaway 1877, type species of *Macrocystella*, has a stem which is divisible into proximal and distal portions; a theca composed of 4 basal, 5 infra-lateral, 5 lateral, 6 radial, and some oral plates; a large periproct surrounded by 5 thecal plates; biserial unbranched brachioles grouped into 5 ambulacra and arising from the margins of the flattened oral surface. In all these respects it agrees with *Mimocystites bohemicus* Barrande 1887, type species of *Mimocystites* which becomes a subjective junior synonym of *Macrocystella*. *Macrocystella azaisi* (Thoral) has 7 orals and thus *Macrocystella* differs from the rhombiferan *Cheirocrinus* Eichwald only in the absence of pectinirhombs. The *Macrocystellidae* are therefore transferred to the rhombiferan superfamily *Glyptocystitida*.

Macrocystella evolved into *Cheirocrinus* by the acquisition of pectinirhombs. In *Macrocystella* respiration probably took place through all the thecal plates which are very thin. In *Cheirocrinus* respiration was restricted to the pectinirhombs thus allowing much thicker and stronger thecal plates to develop.

Macrocystella led a freely vagrant existence and may have had internal buoyancy devices. The stem did not provide permanent fixture and may have been used as a organ of locomotion in conjunction with the brachioles.

THE cystoidea, as currently defined (Kesling 1963) is probably an artificial group. The main character which is used to unite the cystoids as a class is the possession of pore-structures (rhombs and dipores) developed in the thecal plates. However similar pore-structures are found in at least some representatives of other Palaeozoic echinoderm classes (blastoids, crinoids, paracrinoids, eocrinoids, for example) and one genus of rhombiferan cystoids entirely lacks pore-structures. This paper deals with another genus, *Macrocystella* Callaway 1877, which lacks true pore-structures but which is thought to be the oldest known representative of the *Glyptocystitida*, one of the three major rhombiferan superfamilies. *Macrocystella* has a complex taxonomic history (see below) and has been variously regarded as an eocrinoid, a rhombiferan cystoid or as a link between these classes. Close comparison indicates that *Macrocystella* is identical to the rhombiferan genus *Cheirocrinus* Eichwald in all details except the possession of pectinirhombs. Hence *Macrocystella* is regarded as a rhombiferan. It is believed that the absence of pectinirhombs in *Macrocystella* is a primitive character. Many Ordovician pelmatozoans independently developed thecal or calycinal pore structures, apparently in response to respiratory needs. To group all such echinoderms together obscures their true relationships. It is essential to consider other characters in addition to the possession of pore-structures, especially when the latter are so variable.

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Museum, Cambridge and part during the tenure of a Post-doctoral Fellowship at the University of Michigan (NSF grant GB-3366). Both are gratefully acknowledged.

PREVIOUS RESEARCH

Macrocystella (type species *M. mariae* Callaway 1877) was first described from the Lower Ordovician (Tremadoc) Shineton Shales of Shropshire. Barrande (1887, p. 163) described a closely similar genus, *Mimocystites*, for a single species, *M. bohemicus* Barrande. Jaekel (1899, p. 171) suggested that these two genera were synonymous but used the name *Mimocystites*. Jaekel regarded *Mimocystites* as the progenitor of the cystoids and most closely related to the rhombiferan *Cheirocrinus* Eichwald. Bather (1899, p. 920) proposed the family Macrocystellidae which he assigned to the Rhombifera. He did not elucidate the composition of the Macrocystellidae but later (1900, p. 56) included *Macrocystella*, *Mimocystites* and *Lichenoides* Barrande 1887. Although Bather thought *Macrocystella* and *Mimocystites* hardly differed he used both names. Bather's reconstruction of *Macrocystella mariae* (1900, p. 95, fig. 18) was inaccurate in depicting branched arms and considerably influenced subsequent opinions on the affinities of *Macrocystella*.

Jaekel (1918, p. 27) retained both *Macrocystella* and *Mimocystites* (possibly because of Bather's reconstruction of the former) and placed them, with his new genus *Polyptychella*, in the Macrocystellidae. A separate family was proposed for *Lichenoides*. The Macrocystellidae and Lichenoidae were assigned respectively to the orders Plicata and Reducta of the Eocrinioidea. Thorall (1935, p. 113) considered *Macrocystella* and *Mimocystites* to be distinct but based his opinion of the former on the original description. Bassler and Moodey (1943) reverted to Bather's classification, included *Lichenoides* in the Macrocystellidae and that family in the Rhombifera. Cuénot (1948) also assigned *Macrocystella* to the Rhombifera and later (1953) regarded *Mimocystites* as a junior synonym. Moore (1954, p. 127, fig. 2a) published an inaccurate plate diagram of *Macrocystella* which depicts 5 basals, 5 radials, 5 orals, and a minute periproct. Moore regarded *Macrocystella* as an eocrinoid. Sdzuy (1955) accepted *Macrocystella* and *Mimocystites* as separate genera only if published reconstructions were accurate. He based his opinion of *Macrocystella* on Bather's (1900) and Moore's (1954) work, the accuracy of which he doubted. More recently Prokop (1966) and Ubaghs (1968) have suggested that *Macrocystella* and *Mimocystites* are synonymous. Ubaghs regards *Macrocystella* as most closely related to *Cheirocrinus*.

Quite apart from the synonymy of *Macrocystella* and *Mimocystites* another problem arises as to the status of *Cystidea* Barrande 1868. Barrande (1867, p. 179) published two nomina nuda, *Cystidea sedgwicki* and *C. bohemicus*. Later he introduced *C. bavarica* (Barrande 1868, p. 106) this time accompanied by a description and figures. Barrande made it quite clear in both publications that he intended *Cystidea* as a collective group name not a formal generic name and he so used it again (1887), erecting several more species. *Cystidea bavarica* Barrande is a valid binomen and could be construed to be type species of the genus *Cystidea* Barrande by monotypy. Pompeckj (1896, p. 90) and Sdzuy (1955, p. 170) have attributed *Cystidea bavarica* to *Macrocystella*. There is no doubt they are correct in this action and therefore *Cystidea* Barrande 1868, if accepted as an available generic name, should take precedence over both *Macrocystella* and *Mimocystites*. Such action is not in the interests of nomenclatorial stability. No author

has accepted *Cystidea* as a valid generic name whereas *Macrocystella* has been widely used and is figured and described in standard text-books in English, French, and German. Application has therefore been made to the International Commission on Zoological Nomenclature for the suppression of *Cystidea* Barrande 1868 under the Plenary Powers (Paul 1967*b*). In anticipation of a favourable decision, *Macrocystella* is used throughout this work.

The systematics and composition of the Macrocystellidae and the suggested synonymy between *Macrocystella* and *Mimocystites* can only be settled after a revised account of the morphology of *Macrocystella mariae* has been given. Latex impressions of the original specimens of *M. mariae* have been re-examined and additional material studied. This has been compared with Barrande's (1887) and Jaekel's (1899) descriptions and figures of *Mimocystites bohemicus*, with latex impressions of some of Barrande's original material and additional material of *M. bohemicus* in the Schary Collection, Museum of Comparative Zoology, Harvard. Latex impressions of *M. azaisi* (Thoral) have added further information.

Macrocystella and *Mimocystites* are identical and quite distinct from *Lichenoides* to judge from Ubagh's (1953) account of *L. priscus* Barrande. *Polyptychella* Jaekel was founded on isolated plates and its systematic position cannot be settled without further information. The Macrocystellidae thus contains the single genus *Macrocystella*. As previously stated the Macrocystellidae is assigned to the Rhombifera (Glyptocystitida).

SYSTEMATIC PALAEONTOLOGY

Superfamily GLYPTOCYSTITIDA Bather 1899

Diagnosis. A superfamily of Rhombifera with well-developed stem divided into proximal and distal portions; theca composed of 4 basals, 5 infra-laterals, 5 laterals, 4–6 radials, and 7 orals; with pectinirhombs (when pore structures are developed).

All Glyptocystitida are characterized by a theca composed of 25–7 thecal plates arranged in five circlets termed basal, infra-lateral, lateral, radial, and oral. All but two genera—*Macrocystella* and *Amecystis* Ulrich and Kirk—have pectinirhombs. These characters distinguish glyptocystitids from members of the other two major rhombiferan superfamilies, the Hemicosmitida and Caryocystitida. The former have thecal plates arranged in three or four circlets and slightly different rhombs. The latter have a large variable number of plates, some of which may be added during growth, and a completely different type of rhomb (Paul 1968).

Family MACROCYSTELLIDAE Bather 1899 emend. Jaekel 1918

Diagnosis. A family of Glyptocystitida without pectinirhombs; with cylindrical theca having 6 radials; large periproct surrounded by 5 thecal plates and covered with a flexible plated integument; brachioles confined to oral surface, grouped into 5 ambulacra.

Genus MACROCYSTELLA Callaway 1877

1868 *Cystidea* Barrande, p. 106.

1877 *Macrocystella* Callaway, p. 669, pl. 24, fig. 13.

- 1880 *Macrocytella* Callaway; Zittel, p. 420.
- 1887 *Minocystites* Barrande, p. 163, pl. 28 (I), figs. 1–20.
- 1891 *Macrocytella* Callaway; Carpenter, p. 13.
- 1891 *Minocystis* [sic] Barrande; Carpenter, p. 13.
- 1896 *Minocystis* [sic] Barrande; Haeckel, p. 149.
- 1899 *Macrocytella* Callaway; Jaekel, p. 171.
- 1899 *Minocystites* Barrande; Jaekel, p. 172, fig. 33.
- 1900 *Macrocytella* Callaway; Bather, p. 56, fig. 18.
- 1900 *Minocystis* [sic] Barrande; Bather, p. 56.
- 1913 *Macrocytella* Callaway; Springer, p. 157.
- 1918 *Macrocytella* Callaway; Jaekel, p. 27.
- 1918 *Minocystites* Barrande; Jaekel, p. 27.
- 1935 *Minocystites* Barrande; Thoräl, p. 110, 113.
- 1943 *Macrocytella* Callaway; Bassler and Moodey, p. 6.
- 1943 *Minocystites* Barrande; Bassler and Moodey, p. 6.
- 1948 *Macrocytella* Callaway; Regnéll, p. 11.
- 1948 *Macrocytella* Callaway; Cuénot, p. 18, fig. 17.
- 1953 *Macrocytella* Callaway; Cuénot, p. 619.
- 1953 *Minocystites* Barrande; Choubert, Termier, and Termier, p. 137.
- 1954 *Macrocytella* Callaway; Moore, p. 127, fig. 2a.
- 1954 *Minocystites* Barrande; Termier and Termier, p. 92, figs. a–e.
- 1955 *Macrocytella* Callaway; Sdzuy, p. 269.
- 1966 *Macrocytella* Callaway; Prokop, p. 820.

non *Cystidea* Barrande 1867 (nomen nudum) nec Barrande 1887 nec Haeckel 1896 (indeterminate echinoderm fragments).

Diagnosis. As for family.

Regional distribution and stratigraphic range. *Macrocytella* is recorded from the Tremadoc of England and Wales (*M. mariae* Callaway), Bavaria (*M. bavarica* (Barrande) 1868), Bohemia (*M. bohemicus* Barrande 1887), and France (*M. azaisi* (Thoräl) 1935). *Macrocytella* is also recorded from Greenland, the South American Cordillera and Korea (for detailed references see Regnéll, 1948, pp. 11–12). Choubert, Termier, and Termier record *Macrocytella* from the Llandeilo of Morocco. Available specimens confirm the genus from the Llandeilo of Pu-piao, Northern Shan States, Burma, (SM), from the Tremadoc of Mexico (USNM) and possibly from the Caradoc of Corwen, Wales, and Girvan, Scotland (BMNH). *M. pachecoi* Meléndez (1944) from the Ashgill of Aragon, Spain is probably a *Heliocrinites*. *Macrocytella* thus ranges from the Tremadoc to the Llandeilo and possibly Caradoc (Lower–Middle Ordovician).

Macrocytella mariae Callaway 1877

Plate 111, figs. 1, 3–6; Plate 112, figs. 1–3, 5–10; Plate 113, fig. 2

- 1877 *Macrocytella mariae* Callaway, p. 670, pl. 24, fig. 13.
- 1896 *Macrocytella mariae* Callaway; Haeckel, p. 149, pl. 4, fig. 30.
- 1900 *Macrocytella mariae* Callaway; Bather, p. 56, fig. 18.
- 1905 *Macrocytella mariae* Callaway; Fearnside, p. 617.
- 1911 *Macrocytella mariae* Callaway; Kirk p. 16, pl. 2, fig. 17.
- 1913 *Macrocytella mariae* Callaway; Springer, p. 157, fig. 249.
- 1927 *Macrocytella mariae* Callaway; Stubblefield and Bulman, pp. 111, 118.
- 1943 *Macrocytella mariae* Callaway; Bassler and Moodey, pp. 27, 175.
- 1952 *Macrocytella mariae* Callaway; Termier and Termier, p. 363, fig. 9.
- 1953 *Macrocytella mariae* Callaway; Cuénot, p. 618, fig. 15.
- 1955 *Macrocytella mariae* Callaway; Sdzuy, p. 270, pl. 1, fig. 14.
- 1964 *Macrocytella mariae* Callaway; Castell, p. 58, pl. 3, fig. 6.

Diagnosis. A species of *Macrocystella* of small size; with 10–15 brachioles, triangular in section; circular outer proximal columnals with thin, blade-like external flanges.

Type. BU 409 (Pl. 113, fig. 2) is selected as lectotype. It is possibly the original of Callaway 1877, pl. 24, fig. 13 and is from the Shineton Shales of Shineton, Shropshire. Parts of other specimens on this slab are accepted as paralectotypes.

Horizon and locality. Stubblefield and Bulman (1927) record *M. mariae* from the *Clonograptus tenellus* and *Shumardia pusilla* zones (Middle and Upper Tremadoc respectively) of the Wrekin. *M. mariae* is also recorded from the *Shumardia pusilla* zone of Arenig (Fearnside, 1905, p. 617) and *Macrocystella* sp. from the same zone near Portmadoc, Caernarvonshire (Fearnside, 1910, pp. 161–2).

Material. Crushed remains of four more or less complete thecae, one complete stem and many isolated thecal plates and fragments.

Description. A. Stem

The stem has a proximal and a distal portion. One complete proximal portion (Pl. 112, fig. 8) has 20 outer proximals each with a blade-like unornamented external flange. This crushed portion tapers from 5 mm. adorally to 2 mm. in approximately 15 mm. At the junction with the distal stem small distal columnals appear between the flanged columnals. Throughout the preserved portion of the distal stem, flanged and unflanged columnals alternate but this alternation becomes less obvious distally.

The distal portion of the stem (Pl. 111, fig. 1) tapers gradually from 1 mm. proximally to 0.5 mm. at the tip. It is about 35 mm. long. The topmost distal columnal is a thin annulus; the terminal distals are cylindrical and about three times as high as wide. There is no alternation of flanged and unflanged distals in this stem. Preserved proximal stems are straight or quite strongly curved. Curved distal stems are also preserved but there is no evidence to support Bather's (1900) interpretation of the distal stem with a distinct distal coil.

Counterparts of isolated columnals indicate the mode of construction and articulation of the stem. Both proximal and distal portions are composed of two types of columnals. Outer proximals (text-figs. 1a–b) are annular. Each has a smooth, sharp-edged outer flange and a narrow inner flange (text-fig. 2, Pl. 112, fig. 7). Outer proximals alternate with inner proximals and the latter abut against the inner flanges of the former (text-fig. 2). The inner wall of each outer proximal has two sockets set opposite each other on both the upper and lower surfaces. The inner flanges are thickened adjacent to these sockets to form fulcra (text-fig. 2). If the sockets on one surface are orientated N.–S., those on the opposite surface of the same columnal lie NW.–SE. (text-figs. 1a–b). Both upper and lower surfaces of the inner proximals are flattened to form facets,

EXPLANATION OF PLATE 111

Stereophotos of *Macrocystella mariae* Callaway and *M. azaisi* (Thoral)

Figs. 1, 3–6. *M. mariae* Callaway. 1. Complete stem showing proximal and distal portions. BMNH E29113. 3. Left lateral view of crushed theca. BMNH E29110a. 4. Right lateral view of same theca. BMNH E29109a. 5. Anterior lateral view of another crushed theca. BMNH E29109b. 6. Posterior view of crushed theca to show outline of periproct and small periproctal plates. BMNH E29113. Fig. 2. *M. azaisi* (Thoral). Proximal and part of distal stem to show ornament of flanges on outer proximals. BMNH E23697.

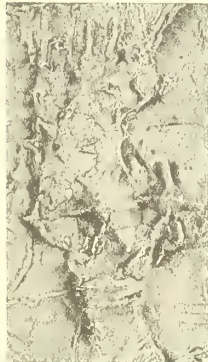
All figures of latex impressions whitened with ammonium chloride sublimate. All $\times 2$.



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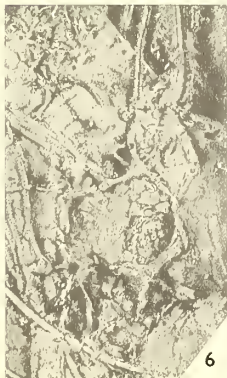
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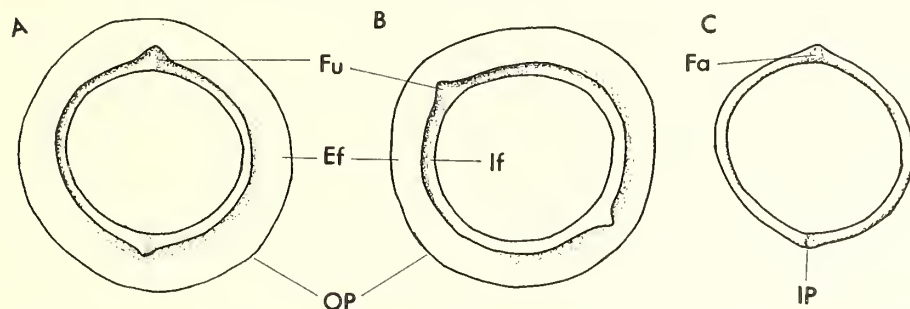
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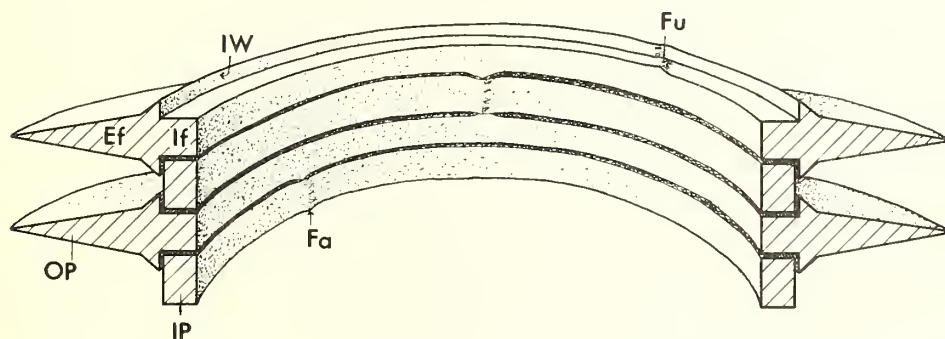
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at the same two opposite points (text-figs. 1c, 2). The outer margin of an inner proximal protrudes at these points and the protrusions key into the sockets in the inner wall of the outer proximals above and below (text-fig. 2). The fulcras on the outer proximals and the facets on the inner proximals articulate and the axis of articulation changes by approximately 45° with each outer proximal. This results in a right-handed spiral arrangement of articulation facets in *M. azaisi* and presumably in other *Macrocyrella*.



TEXT-FIG. 1. Proximal stem columnals of *Macrocyrella mariae* Callaway. a, b. Opposite sides of one outer proximal columnal (OP) in the same orientation to show different orientations of fulcras (Fu). c. Inner proximal columnal (IP). Ef, external flange; Fa, facet; If, internal flange.



TEXT-FIG. 2. Diagrammatic reconstruction of part of proximal stem of *Macrocyrella mariae* Callaway to show arrangement of outer (OP) and inner (IP) columnals and spiral arrangement of facets (Fa) and fulcras (Fu). Ef, external flange; If, internal flange; IW, inner wall of outer proximal columnal. This has been drawn as a left-handed spiral although *M. azaisi* is known to show a right-handed spiral.

Each inner proximal is keyed into the sockets of the outer proximals above and below. Thus although highly flexible, the stem was quite resistant to rotation about its axis. Both inner and outer proximals are annular and the proximal stem has a wide lumen. Flexing of the proximal stem was probably achieved by muscles housed in this lumen. The mechanical keying of the columnals prevented rotation which would have sheared such muscles.

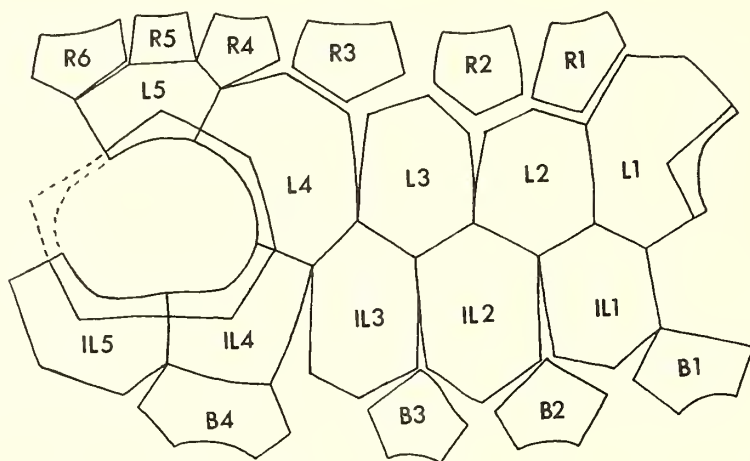
Larger (sometimes flanged) and smaller (unflanged) distals alternate in the distal stem but this becomes less apparent distally. The most proximal distals, which appear to be

newly formed, are annular but most distals are cylindrical. All distals have narrow lumina and the articulating surfaces are smooth (Pl. 112, fig. 3).

The nature of the outer proximals may prove to be a useful specific character. In *M. mariae* the outer proximals are approximately circular with thin, blade-like outer flanges (Pl. 111, fig. 1, Pl. 112, fig. 7). In *M. bavarica* the outer flanges are also thin and sharp-edged but are produced into ten angles or incipient spines (Sdzuy, 1955, pl. 1, figs. 8–10, text-fig. 1h). In *M. azaisi* the outline is circular but the flanges are thicker and have fine irregular granules or spines encircling them (Pl. 111, fig. 2, Pl. 113, figs. 1, 8). The outer flanges of *M. sp. nov.* from Mexico have four rounded lobes arranged in two pairs.

B. Theca

All known thecae are crushed and it is impossible to describe all thecal plates from one specimen. BMNH E29109–10 are counterparts which show two crushed thecae in different orientations. There is another theca which shows details of the periproct.

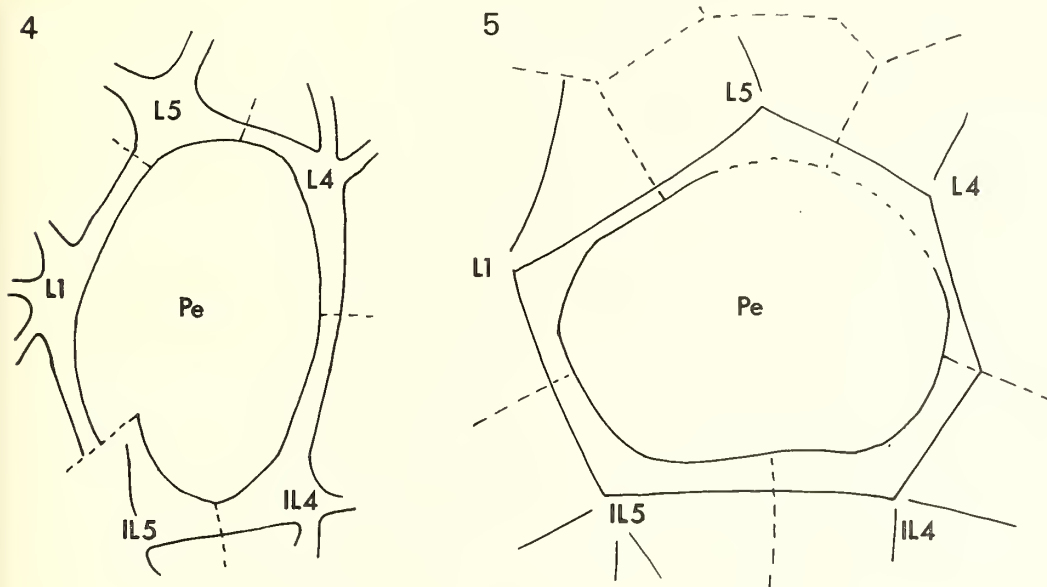


TEXT-FIG. 3. Diagrammatic reconstruction of plate arrangement of *Macrocystella mariae* Callaway. Based on BMNH E29109a–b, E29110a–b, and E29113. B1–B4 basals, IL1–IL5 infra-laterals, L1–L5 laterals, R1–R6 radials.

A composite plate arrangement and a reconstruction based on these specimens are depicted in text-figs. 3 and 15. The theca was composed of five circlets of plates, four of which can be seen in *M. mariae*. The subvective system was confined to the oral surface from the margins of which the brachioles arose in five groups.

Some details of text-fig. 3 are restored but all plates shown existed. The four basals (BB) unite aborally to form an invagination around the stem. One basal (presumably B4) was hexagonal (Pl. 112, fig. 2). The infra-laterals (ILL) form a closed circlet; IL4 and IL5 contribute to the periproct border. IL1, IL2, and IL3 are roughly hexagonal. The five laterals (LL) apparently form a closed circlet; L1, L4, and L5 contribute to the periproct border. L5 is distinctly smaller than the other laterals and has a radial (R5)

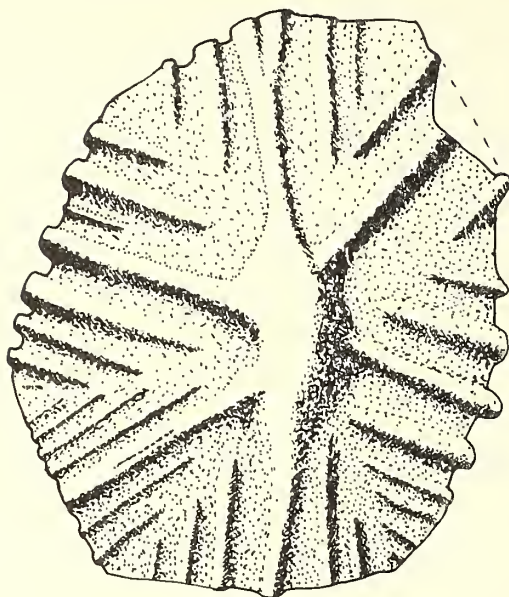
directly adoral to it. One pair of counterparts (Pl. 111, figs. 3, 4) seem to have three hexagonal laterals which means either there were six laterals in this specimen or only L1 and L5 contributed to the periproct border. Unfortunately the relevant portion of this theca is crushed and this appearance may be misleading. The six radials (RR) form a closed circlet; one is directly adoral to L5. There are seven orals (OO) in *M. azaisi*.



TEXT-FIGS. 4-5. Camera lucida drawings of the periproct (Pe) of *Macrocyrella mariae* Callaway. 4. BMNH E29110b cf. Pl. 2, fig. 9. 5. BMNH E29113 cf. Plate 1, fig. 6. IL4-IL5 infra-laterals, L1, L4, L5 laterals.

The mouth, gonopore, and hydropore have not been detected in *M. mariae* but were all on the oral surface in *M. azaisi* (text-figs. 11a, b). Critical details of the periproct show in BMNH E29110b, and more clearly, in BMNH E29113 (text-figs. 4, 5). There are five plates around the periproct which is large. The periproct was covered by a thin, flexible, plated integument in life. Some small periproctal plates are preserved (Pl. 111, fig. 6) but the position of the anal pyramid is unknown.

The outlines of the individual thecal plates vary with their positions in the theca. Periproct border plates can be recognized easily, as can basals and radials. The remaining five laterals and infra-laterals are difficult to distinguish from each other. All plates have raised umbones from which ridges radiate to the middles of the sides, connecting centres of adjacent plates (text-fig. 6). Auxiliary ridges are developed parallel to the primary ridges to form 'rhombs'. These 'rhombs' are not true rhombs as they are composed of folds in the thecal plates. There is no development of thin-walled thecal canals. The external ridges of *Macrocyrella* are formed by the folds in the plates and are not solid strengthening struts such as occur in *Cheirocrinus*. The thecal plates of *M. mariae* are approximately 0.1 mm. thick.



TEXT-FIG. 6. Isolated thecal plate of *Macrocyrtella mariae* Callaway to show folds. BMNH E29119.

c. Subvective system

The exothecal portion of the subvective system consists entirely of brachioles. These are long, slender, biserial, unbranched structures. The most complete brachioles (Pl. 112, fig. 10) have approximately 120 brachiolar plates and are slightly longer than the thecal height (up to 16 mm.). The brachioles have a triangular cross-section with sides twice the width of the adoral surface (text-fig. 7). The food groove ran down the centre of the adoral surface and was covered by lappets in life. The lappets are between one and a half times and twice as numerous as the brachiolars and apparently were flexible. Some have been preserved covering the food groove; others in an 'open' position (Pl. 112, fig. 10). The lappets alternate and each one imbricates over its more distal neighbour (text-fig. 8).

EXPLANATION OF PLATE 112

Figs. 1-3, 5-10. *M. mariae* Callaway. 1. Internal and external views of two isolated thecal plates. The internal view (above) shows the folds in the plates. The other plate was one of five bordering the periproct (probably L1). BMNH E29112, $\times 5$. 2. External view of B4 and an isolated distal columnal. BMNH E29112, $\times 5$. 3. Three isolated thecal plates. All originally bordered the periproct. BMNH E29112, $\times 5$. 5. Internal mould of isolated thecal plate BMNH E29119, $\times 3$. 6. Inner proximal columnal within outer proximal columnal. BMNH E29112, $\times 2$. 7. Outer proximal columnal showing inner flange and fulcra. BMNH E7574, $\times 1.5$. 8. Crushed stem and theca. Note the larger distals are flanged. BMNH E7574, $\times 1.5$. 9. Stereophotos of posterior lateral view of crushed theca showing periproct. Counterpart to Plate 1, fig. 5. BMNH E29110b, $\times 2$. 10. Detail of brachioles to show lateral, ab- and adoral views. BMNH E29109, $\times 3$.

Fig. 4. *M. azaisi* (Thoral). Lateral view of theca and stem. BMNH E23697, $\times 2$.

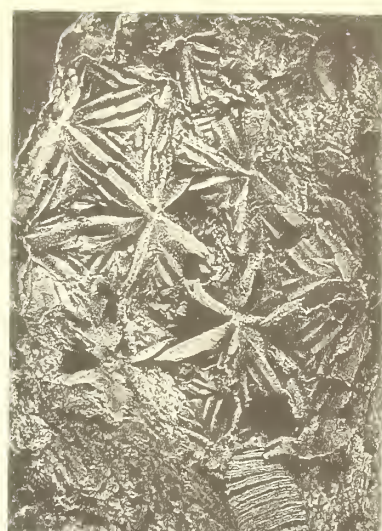
All except Fig. 5 latex impressions, all whitened with ammonium chloride sublimate.



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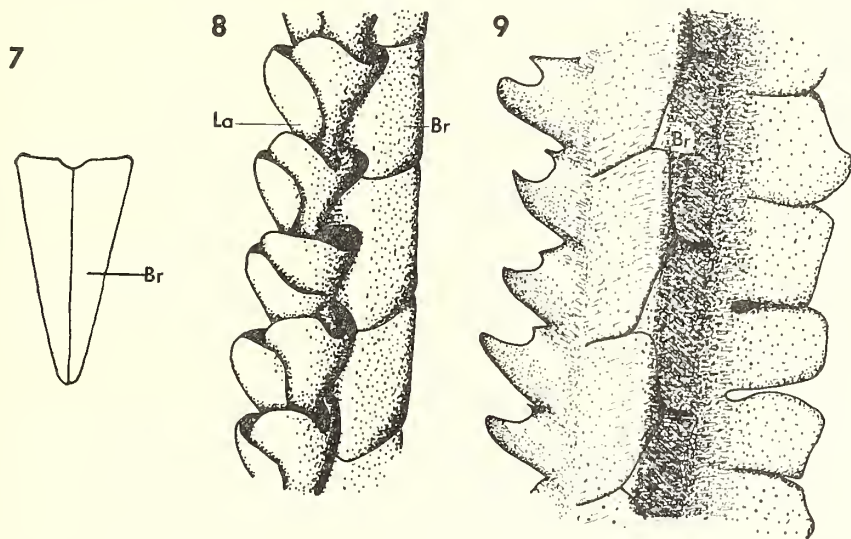
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10



They coalesce towards the margins of the brachiole to form a continuous narrow band (text-fig. 9). The free portions were able to curl in on themselves. This curling in is not preservational and the lappets may have been only partially calcified in life.



TEXT-FIGS. 7-9. Brachioles of *Macrocyrella mariae* Callaway. 7. Diagrammatic section through brachiole without lappets. 8. Camera lucida drawing of portion of brachiole with lappets (La) closed over food groove. Note that the lappets alternate and imbricate. 9. Camera lucida drawing of aboral view of brachiole with lappets in 'open' position. Br brachiolar plate. Text-figs. 8-9 based on BMNH E29113.

No more than three brachioles arise in any one ambulacrum and there were presumably 10-15 brachioles in all. There is no evidence to support Bather's (1900, fig. 18) reconstruction of branched brachioles. BMNH E29110a shows three brachioles in one radius (Pl. 111, fig. 3): all three are separate entities from their origin at the margin of the theca.

Macrocyrella mariae Callaway is characterized by the following: 1. A stem which is divisible into two portions: a short, rapidly tapering, highly flexible, proximal portion composed of two types of annular columnals with a wide lumen; and a long distal portion composed of cylindrical columnals with a narrow lumen.

2. A theca with plate formula 4BB, 5ILL, 5LL, 6RR, ?OO.

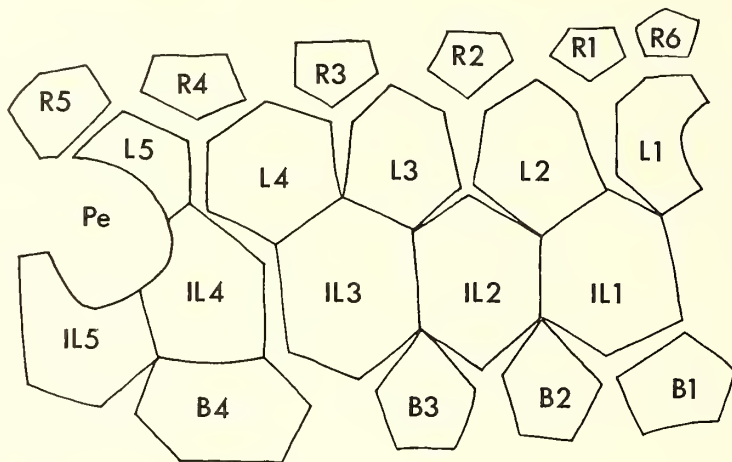
3. A large periproct surrounded by five thecal plates and covered with a flexible plated integument.

4. Biserial, unbranched brachioles which arise from the margins of the flat oral surface and are grouped into five ambulacra.

COMPARISON WITH *MIMOCYSTITES* BARRANDE

Mimocystites bohemicus Barrande has a subjective system which is confined to the flat oral surface and consists of about twenty brachioles grouped into five ambulacra.

Three brachioles were present in one radius of an available specimen (UC latex impression of original of Barrande 1887, pl. 28 (1), fig. 14). The theca is composed of 4BB, 5ILL, 5LL, 6RR, and some OO. Jaekel's analysis of the arrangement of thecal plates (1899, p. 201, fig. 36) is reproduced here in a slightly modified form (text-fig. 10). This interpretation differs slightly from that of *Macrocystella mariae*. Only two laterals



TEXT-FIG. 10. Jaekel's (1899) interpretation of the plate arrangement of *Mimocystites bohemicus* Barrande with modern notation of plates. B1-B4 basals, IL1-IL5 infra-laterals, L1-L5 laterals, R1-R6 radials. Cf. text-fig. 3.

(L1 and L5) contribute to the periproct border and L1 has a straight upper border with R6 directly adoral to it. This is an unexpected arrangement. Two specimens in the Schary collection (MCZ) apparently show the arrangement figured for *Macrocystella mariae*. However one specimen of *M. mariae* (Counterparts BMNH E29109a and 29110a) has apparently three hexagonal laterals as shown in Jaekel's figure of *Mimocystites bohemicus*. It seems possible that the plate arrangement varied slightly in different specimens. *Mimocystites azaisi* Thoral has a plate arrangement identical to that in *Macrocystella mariae*. Both the present and Jaekel's interpretations agree in most respects, particularly in the five plates around the periproct.

EXPLANATION OF PLATE 113

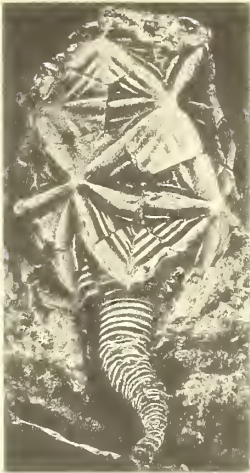
Stereophotos of *M. mariae* Callaway, *M. azaisi* (Thoral) and *M. azaisi multicristata* (Thoral).

Fig. 2. *M. mariae* Callaway. Lateral view of lectotype. BU 409.

Figs. 1, 3, 5, 8. *M. azaisi* (Thoral). 1. Anterior lateral view of theca to show well-developed folds in B2 and ornament of stem flanges. CU. 3. Lateral view of another theca. CU. 5. Oral view of same. 8. Lateral view of another theca to show well-developed folds in B2 and ornament of stem flanges. CU.

Figs. 4, 6, 7. *M. azaisi multicristata* (Thoral). 4. Oblique oro-lateral view to show ornament of orals and lateral food grooves alternating in ambulacrum IV (left). CU. 6. Interior view of oral surface of same theca. 7. Lateral view of same theca to show more strongly developed folds in radial plates.

All figures of latex impressions whitened with ammonium chloride sublimate. All $\times 2$.



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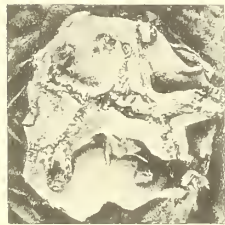
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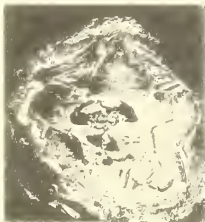
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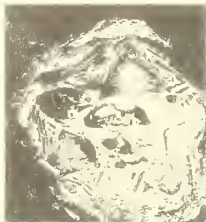
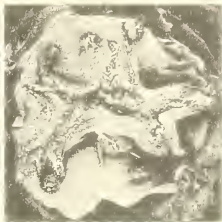
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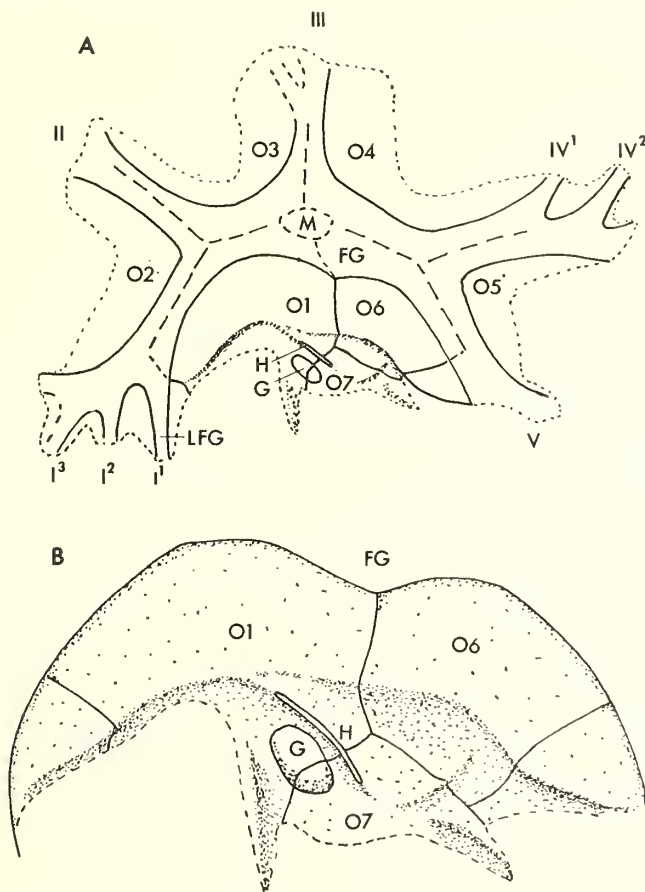
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The thecal plates of *Mimocystites bohemicus* and *M. azaisi* are identical to those of *Macrocybella mariae* except in the number of folds, which is variable in each species.

The proximal stem of *Mimocystites bohemicus* is identical to that of *Macrocybella mariae* except that the outer proximals have thicker flanges which are less blade-like. *Mimocystites azaisi* has still thicker flanges, the peripheries of which are granulose or spinose (Pl. 111, fig. 2, Pl. 113, figs. 1, 8).

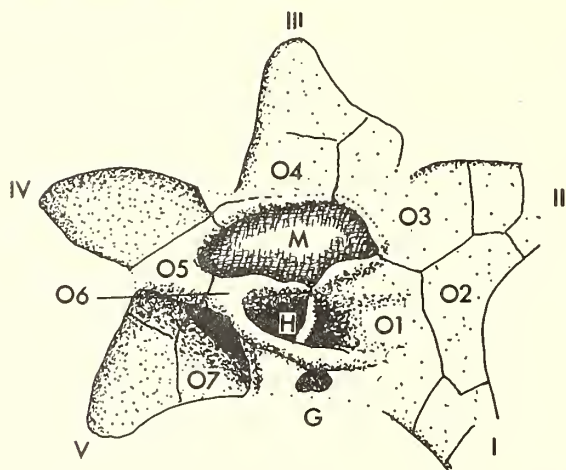


TEXT-FIG. 11. Camera lucida drawing of oral surface of *Macrocybella azaisi* (Thoral). *a*, entire surface to show oral plates and arrangement of food grooves. Cf. Plate 113, fig. 5. CU. *b*, detail of gonopore and hydropore area of same. FG, food groove; G, gonopore; H, hydropore; LFG, lateral food groove; M, position of mouth which was probably much larger than shown; O1-O7, orals. I-V, ambulacra; I¹, I², I³, facets of ambulacrum I; IV¹, IV², facets of ambulacrum IV.

The type species and one other species of *Mimocystites* therefore exhibit all the features which characterize *Macrocybella mariae*. All three are congeneric.

Specimens from the Montagne Noire, France (UC latex impressions) have yielded additional information on the morphology of *Macrocybella*. One example of *M. azaisi* (Thoral) has an almost complete oral surface (text-fig. 11a, Pl. 113, fig. 5). Another

example of *M. azaisi multicristata* (Thoral) shows both the internal and external surfaces of the oral area (text-fig. 12, Pl. 113, figs. 4, 6). There were seven orals, arranged as shown in text-fig. 11a. A slit-like hydropore and an oval gonopore are developed across the common suture of O1 and O7 (text-fig. 11b). There are five main ambulacral grooves each of which has lateral branches leading to brachiole facets. Apparently the branches are consistently to the left of ambulacra I and IV in the example of *M. azaisi* (Pl. 113, fig. 5) but regularly alternate in ambulacrum IV in the example of *M. azaisi multicristata* (Pl. 113, fig. 4). Details of the other ambulacra are not well preserved in either specimen.



TEXT-FIG. 12. Camera lucida drawing of internal oral surface of *Macrocystella azaisi multicristata* (Thoral). cf. Plate 113, fig. 6. CU. G, supposed internal opening of hydropore; H, supposed internal opening of gonopore; M, mouth; O1–O7, orals; I–V ambulacra.

In internal view the mouth is large (4.6 mm. $\times$ 1.7 mm.) and is covered by ambulacral cover plates. The orals and ambulacral flooring plates are visible (Pl. 113, fig. 6). The latter are between, not on, the orals and form part of the thecal wall. Only primary ambulacral flooring plates can be detected. Close to the mouth is a deep pit which apparently connected to the hydropore. This pit is separated from the mouth and the supposed gonopore by two internal ridges, one on each side. The gonopore is apparently represented by a small circular pit some distance from the mouth (text-fig. 12). Unfortunately the critical area of the external oral surface is not preserved and it is not possible to match up external and internal openings. Ambulacra IV

and V are more deeply impressed than I, II, and III. Another pit is developed obliquely under the aboral of the two internal ridges near the hydropore (Pl. 113, fig. 6). The significance of this is unknown.

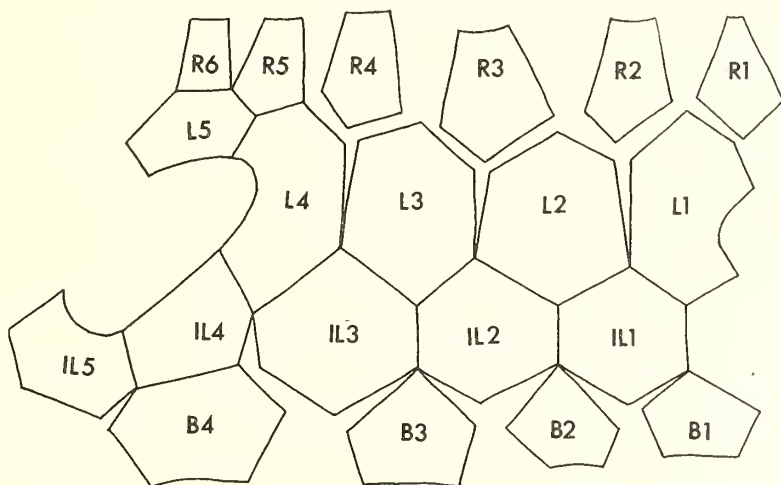
COMPARISON WITH OTHER PELMATOZOA

Several authors have grouped *Macrocystella* with *Lichenoides* while others have placed them in separate families. In addition *Macrocystella* has been variously assigned within the Pelmatozoa.

The most recent and most complete account of the morphology of *Lichenoides* is that of Ubaghs (1953) who showed that it completely lacks a stem. The thecal plates are arranged in four circlets but the total number is variable, 5–12 basals, 5 infra-laterals, 5–7 laterals, and 5–7 radials. (The homologies with the Glyptocystitida implied by the use of the same terms for the plate circlets are unjustified.) All the infra-laterals, laterals, and radials bear epispines. These are a type of pore-structure with a single sutural pore which leads to a narrow channel in the external surface of both adjacent plates (see

Ubaghs 1953, figs. 3, 11). There is no lateral periproct in *Lichenoides*. The brachioles arise from both lateral and radial plates and apparently they are not grouped into five radii.

Thus while *Lichenoides* resembles *Macrocybella* in having definite plate circlets and biserial, unbranched brachioles it differs in the absence of a stem and lateral periproct, in the presence of epispires and brachioles on lateral and radial plates, and in the total number and position of the thecal plates. These differences are considered to be important taxonomically. The Lichenoidae and Macrocybellidae are maintained as separate families as suggested by Jaekel (1918) and Ubaghs (1953).



TEXT-FIG. 13. Plate arrangement in *Cheirocrinus radiatus* Jaekel. Based on Jaekel, 1899, p. 213, fig. 36. B1-B4, basals; IL1-IL5, infra-laterals; L1-L5, laterals; R1-R6, radials.

Among cystoids *Macrocybella* most closely resembles *Cheirocrinus* Eichwald. This latter genus is characterized by a stem with proximal and distal portions. The construction and articulation of the stem are identical to that of *Macrocybella* and the helical arrangement of the articulations of the proximal stem was described by Billings (1858) in *Cheirocrinus anatififormis* (Hall) (= *Glyptocystites logani* Billings).

The theca of *Cheirocrinus* is composed of 27 plates arranged in 5 circlets: 4BB, 5ILL, 5LL, 6RR, and 7OO. The periproct is large, surrounded by 5 thecal plates (IL4, IL5, L1, L4, and L5) and was covered by a flexible plated integument in life. L5 is directly adoral to the periproct and has R5 directly adoral to it (text-fig. 13). The subvective system is restricted to the flat oral surface and there are 20-5 brachioles grouped into 5 ambulacra whose flooring plates lie between the orals, not on them. *Cheirocrinus* differs from *Macrocybella* in the possession of pectinirrhombs.

Macrocybella and *Cheirocrinus* have in common many distinctive features of which perhaps the most important is the detailed structure of the stem. This type of stem is characteristic of and confined to the superfamily Glyptocystitida. It is most unlikely that such a complex organ developed independently in two groups which share other common characteristics. *Macrocybella* probably gave rise to *Cheirocrinus* and through it to the other Glyptocystitida as originally suggested by Jaekel (1899).

Thoral (1935) thought it possible to recognize in the Montagne Noire a lower horizon with *Macrocyrtella azaisi* (upper Tremadoc) and a higher horizon with *Cheirocrinus languedocianus* (basal Arenig). In Britain *M. mariaae* occurs below the oldest *Cheirocrinus*. *Macrocyrtella* seems to be a characteristic fossil of the Tremadoc whereas the oldest known *Cheirocrinus* are all Arenig. Stratigraphic evidence agrees with the idea that *Macrocyrtella* evolved into *Cheirocrinus*.

In the past the main objections to the inclusion of *Macrocyrtella* in the Rhombifera were its branched arms and lack of rhombs. The former was an error but the latter is more important. Regnéll (1945) has stressed that the main character which unites the cystoids as a class is the presence of pore-structures. Detailed study of cystoid pore-structures (Paul, 1968) suggests the Rhombifera should be regarded as a distinct class. The rhomb-less *Macrocyrtella* is included in the Rhombifera on the same grounds that led Kesling (1963) to include *Amecystis* in the Rhombifera. *Amecystis* is effectively a *Pleurocyrtites* without pectinirhombs, just as *Macrocyrtella* is a *Cheirocrinus* without pectinirhombs. The many similarities outweigh this single distinction.

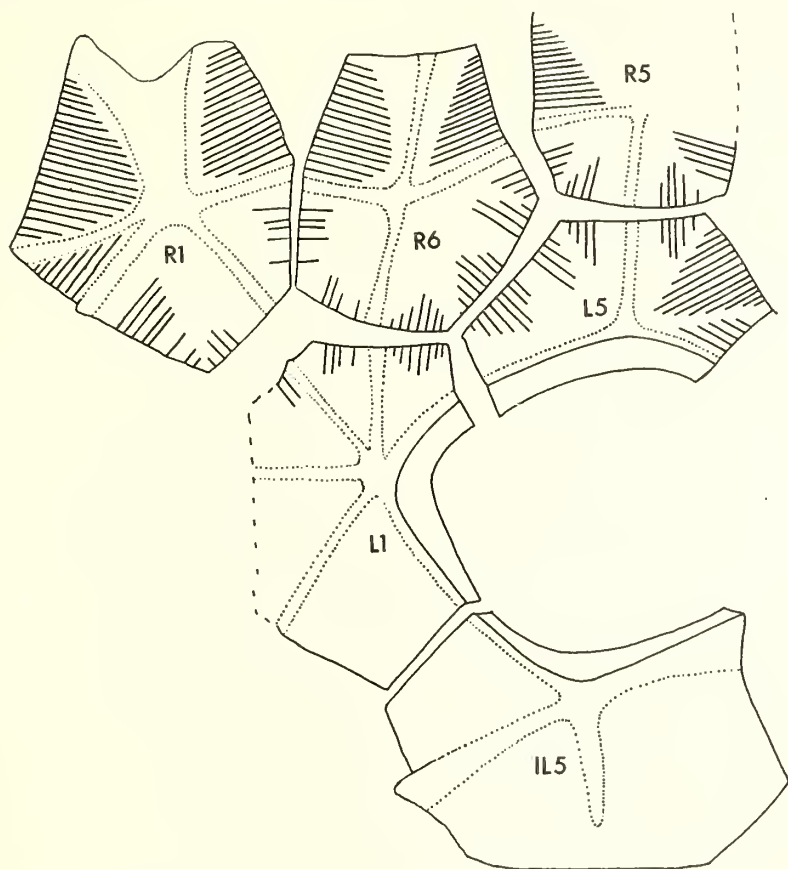
THE EVOLUTION OF PECTINIRHOMBS

The rhombs of *Cheirocrinus* are fully developed pectinirhombs (which Bather regarded as a highly specialized type of rhomb) even in the earliest species known. There is no evidence of a gradual evolution of pectinirhombs. If *Macrocyrtella* evolved into *Cheirocrinus*, pectinirhombs either appeared 'suddenly' or pre-existing structures broke through the thecal plates to appear as pectinirhombs. The internal surfaces of isolated plates in both *Macrocyrtella* and *Cheirocrinus* show no features which could be incipient pectinirhombs. Pectinirhombs were functional throughout their growth; they are present as external features from the earliest stages. They did not develop internally and become external features later in growth. Rather sudden appearance therefore seems more likely.

All rhombs have generally been accepted as respiratory organs. In the simplest case respiration would have taken place through the thecal wall. The amount of oxygen required would have been proportional to the volume, and the amount of respiratory exchange to the surface area, of the theca. The oxygen requirements would thus increase with growth faster than the amount of exchange. This difficulty can be overcome, without materially altering the over-all thecal shape, by the production of evaginations or invaginations of the thecal wall. *Macrocyrtella* has the former in the folds of the thecal plates. The dichopores of pectinirhombs are invaginations and produce a slightly better volume to surface area ratio.

Exchange is facilitated by a large surface area and a thin exchange surface. Either invaginations or evaginations are almost equally effective in increasing the surface area but the latter are exposed and liable to mechanical damage. The ridges in the thecal plates of *Macrocyrtella* probably facilitated exchange by increasing the surface area. The thecal plates were extremely thin (0.1 mm.) and although strengthened by the ridges they were still very fragile. The dichopores of pectinirhombs are within the theca and therefore protected. Dichopore walls are much thinner than thecal plates (usually 0.01 mm.). In *Macrocyrtella* the entire thecal wall probably took part in exchange. In *Cheirocrinus* a differentiation of function is seen. Without decreasing the amount of exchange it

became possible to have much thicker and stronger thecal plates. Exchange was restricted to specialized areas, namely the pectinirhombs. The thecal plates of *Cheirocrinus*, especially in early species like *C. languedocianus*, are still thin compared with later glyptocystitids but they are thicker (usually more than 0.5 mm.) than those of *Macrocybella*.



TEXT-FIG. 14. Pectinirhombs of a specimen of *Cheirocrinus languedocianus* Thor. Note the incomplete pectinirhombs. Based on camera lucida drawings of the individual plates. CU. Symbols as in text-fig. 3.

In *Macrocybella* all thecal plates are ridged and all probably contributed to respiration. However the distribution of ridges in *M. azaisi* is uneven. More and better-developed ridges occur on radial plates (Pl. 113, fig. 7) and associated with B2 (Pl. 113, figs. 1, 8). This is quite independent of the variation between *M. azaisi* and *M. azaisi multicristata*. Sdzuy (1955, figs. 1d-g) figured a similar concentration of ridges on B2 in *M. bavarica*. In *Cheirocrinus languedocianus*, probably the earliest known species of *Cheirocrinus*, dichopores are developed across more sutures than in later species (text-fig. 14). Many sutures bear one or two demi-rhombs and some have only a few randomly spaced dichopores. These latter form incomplete pectinirhombs which have not been recorded in later glyptocystitids. Clearly the arrangement is more random than

in later species which have a reduced number of pectinirrhombs. All species of *Cheirocrinus* have pectinirrhombs on radials and on B2 however. The similarity between the distribution of ridges in *Macrocystella* and of pectinirrhombs in *Cheirocrinus* indicates a concentration of respiratory activity in the same areas of their thecae, probably reflecting a similar internal organization, and confirming the idea that *Macrocystella* and *Cheirocrinus* are related.

MODE OF LIFE

The stem of *Macrocystella* lacks a root structure or anchoring device and there is little evidence for Bather's reconstruction of a distal coil to the stem. Whatever benefits were conferred on *Macrocystella* by the possession of a well-developed stem, they were not associated with permanent attachment. *M. mariae* and other species of *Macrocystella* are found in fine-grained sediments in which there is little evidence for suitable attachment surfaces. Nevertheless the general morphology of the theca and subvective system suggests *Macrocystella* habitually held its theca upright. Only free-floating or free-swimming modes of life can satisfy both lines of reasoning.

The distal stem in *Macrocystella* and in other early glyptocystitids tapers gradually to a small diameter and ends abruptly. The terminal portion of the stem is not modified as in *Brockocystis* Foerste or *Lepocrinites* Conrad and there is no way to be certain that the last distal columnal preserved was the terminal columnal in life. It is possible that *Macrocystella* broke free prior to death and was buried some distance from its point of attachment. However *M. mariae* and other apparently free glyptocystitids are frequently preserved in clay-grade sediments with little associated fauna which could have acted as substrata for attachment. No *Macrocystella*, *Cheirocrinus* nor *Pleurocystites* has ever been found with a root structure or anchoring device, yet many specimens are excellently preserved with brachioles, periproctal membranes, and other delicate structures intact. Some specimens from the Trenton Limestone of Ottawa and the Starfish Bed of Girvan, Scotland (for example) suggest that death was due to burial alive and therefore that the specimens are complete. The terminal diameter of the distal stem (0.5 mm.) compared with the total length (50 mm.), in *M. mariae* indicates that if attached the stem was extremely weak at this point. *Macrocystella* may have been attached early in its development but the evidence strongly suggests that it was free for the major portion of its life.

Pentameral symmetry is well developed in *Macrocystella*: there are circlets of five plates and five ambulacra. The theca is cylindrical not flattened on one side. Bather argued that pentameral or radial symmetry was developed in fixed animals and he associated departures from pentamery in echinoderms, particularly flattening of the theca, with departures from an upright fixed position. *Pleurocystites*, another free glyptocystitid, has a markedly flattened theca which apparently lay on the sea floor. If *Macrocystella* and *Cheirocrinus* also lay on the sea floor one would expect a similar flattening of their thecae. The persistence of *Macrocystella* and *Cheirocrinus* after the appearance of *Pleurocystites* suggests the former were adapted to a different mode of life. The subvective system in *Macrocystella* and *Cheirocrinus* is confined to the oral surface and forms a cone of collection. Paul (1967a) suggested that such an arrangement is better adapted to collect floating food particles in a relatively still sea and requires an upright theca. Both *Macrocystella* and *Cheirocrinus* have respiratory surfaces developed

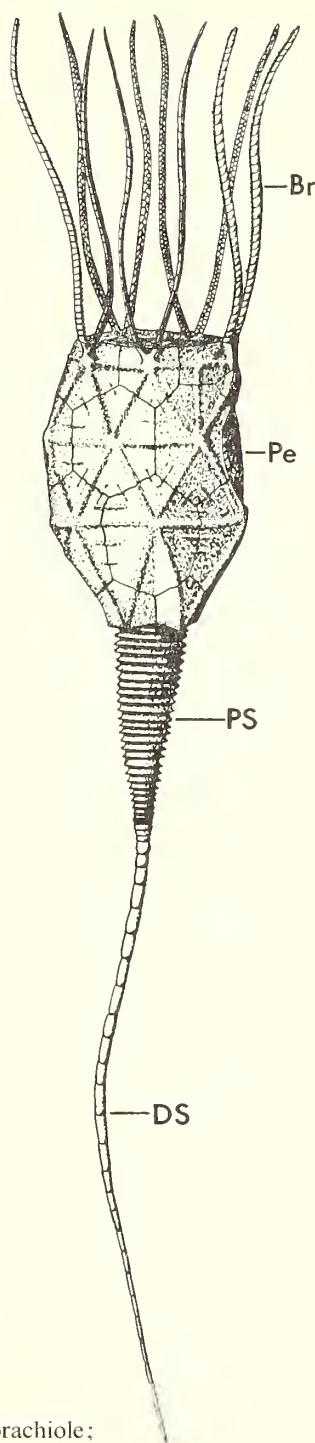
all round the theca and some of these would have been fouled if the theca rested on the sea floor. *Pleurocystites* however has all its pectinirhombs on one side of the theca, presumably the upper side in life. All these lines of evidence indicate that *Macrocystella* and *Cheirocrinus* habitually held their thecae upright. However, when upright, *Macrocystella* is very top heavy (text-fig. 15) and the theca would have rested on the sea floor if the stem were free.

Without a root structure or anchoring device the stem could exert no leverage against the substrate and would have been useless to maintain the theca upright. The distal stem may have been partially buried in the substrate but its whiplike form would provide little resistance in soft mud. There is no evidence for partial burial of the stem during life in specimens which apparently died by entombment. Other pelmatozoans which were fixed in soft sediments have well-developed branching root structures (e.g. *Eucalyptocrinites* and *Caryocrinites*). Even recent brachiopods which live in soft sediments have branching root-like pedicles. If *Macrocystella* and *Cheirocrinus* were free and habitually held their thecae upright they could only achieve this if they floated or swam actively. Both modes of life are known in other pelmatozoans.

Recent free-swimming crinoids have negative buoyancy (i.e. they are denser than sea water) and this has generally been assumed to obtain in all echinoderms. If the coelomic fluids and organic tissues are of neutral buoyancy, the only element which contributes to negative buoyancy is the skeleton, the effective density of which is 0.8 gm. per cc. when fully immersed in sea water. An echinoderm with negative buoyancy will sink when at rest. Recent free crinoids maintain their position by swimming. They are characterized by a well-developed subvective system with multiple branched arms and, in most cases, by the complete absence of a stem and marked reduction of the calyx: certainly none has a calyx comparable in size to a cystoid theca. Swimming is wholly achieved by the arms, buoyancy devices are absent (there is nowhere to house them) and dead weight in the form of stem and thecal plates is minimal.

In *Macrocystella* there is a relatively undeveloped subvective system, a large theca, and a well-developed stem. Dead weight was considerable and the brachioles may have been relatively inefficient organs of locomotion. The flattening of the brachioles in *M. mariae* is in the opposite direction to that one would expect if they were used actively in swimming.

TEXT-FIG. 15. A reconstruction of *Macrocystella mariae* Callaway. Br, brachiole; DS, distal stem; Pe, periproct; PS, proximal stem.



However if the lappets were folded in during an upstroke and extended during a downstroke the brachioles could have been fairly efficient swimming organs. The relatively large theca has very thin plates and could well have housed buoyancy devices. Quite small gas bubbles would have significantly altered the total buoyancy: in *M. mariae* a bubble 3 mm. in diameter would completely compensate for the weight of a theca 10 mm. in diameter and 15 mm. high. *Brockocystis* Foerste, another apparently free glyptocystitid, has hollow, bulbous thecal plates each of which could have housed a gas bubble. The stem bulb in *Brockocystis* is also hollow. It is not impossible that *Macrocystella* had buoyancy chambers but there is no direct evidence for this.

Function of the stem. Most authors, with the notable exception of E. Kirk (1911), have taken stems in pelmatozoans to imply permanent fixture. It is therefore surprising to find among early stemmed pelmatozoans an almost total lack of definite root structures or anchoring devices. What benefit did the possession of a stem confer if it was not attachment?

If an ancestral stem-less form were permanently attached, the development of a stem could have raised the theca off the substrate. This would reduce the chances of accidental burial, of fouling by mud-laden currents, and it could have placed the echinoderm above other benthonic organisms competing for food particles as suggested by Kesling and Mintz (1961). What may have been attempts to raise the theca, or at least the oral surface, are seen in edrioasteroids and some diploporites but none of these produces a true stem, only aboral stem-like projections of the theca. Alternatively if an ancestral stem-less form were free, a stem would weight the theca aborally. This would maintain the animal upright if the theca were buoyant or if the subvective system were used in swimming. However, a simple weight placed aborally would satisfy this requirement.

The form of the stem in *Macrocystella* could have allowed considerable variation in buoyancy when the stem was in contact with the substrate. If the theca was buoyant but the weight of the stem gave the whole animal negative buoyancy, equilibrium could have been reached if part of the stem rested on the sea floor. The flexible proximal stem would still allow the theca to be held upright; buoyancy would hold the theca upright without any effort on the part of the animal. *Macrocystella* probably rested with its theca near but not on the substrate and moved about by means of its brachioles and stem. This interpretation seems preferable to one without a buoyant theca even though there is no direct evidence for buoyancy devices. If *Macrocystella* used its brachioles to maintain an upright posture it could not have rested in an upright position. As recent free crinoids feed when at rest it is difficult to imagine how *Macrocystella* fed under these circumstances.

Macrocystella is imagined to have had a slightly buoyant theca but to have been weighed down by the stem. Under these circumstances it could have rested with the stem on the sea floor, the theca upright and the brachioles extended to feed. In times of short food supply *Macrocystella* swam away actively by means of its brachioles and stem, moving just above the sea floor. *Macrocystella* may have drifted under the influence of gentle currents but current action was not strong in the environment of deposition of *M. mariae*. Occasionally *M. mariae* was overwhelmed by a sudden influx of mud possibly brought about by turbidity currents. *Macrocystella* seems to have lived in much deeper water than most later glyptocystitids (see Paul 1967a).

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C. R. C. PAUL
Geology Department
Indiana University Northwest
Gary, Indiana

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A REVISION OF SOME UPPER DEVONIAN FORAMINIFERA FROM WESTERN AUSTRALIA

by JAMES E. CONKIN and BARBARA M. CONKIN

ABSTRACT. Arenaceous foraminifera described by Crespin (1961) from the Upper Devonian Virgin Hills and Gogo Formations of the Fitzroy Basin of Western Australia are revised. Four genera and eight species are recognized; these include *Oxinoxis* Gutschick 1962 and *Sorosphaeroidea* Stewart and Lampe 1947, which were previously recorded only from the Middle Palaeozoic of the United States. The similarity of the fauna to Upper Devonian foraminiferal faunas in the United States and Europe is described.

Several new occurrences of foraminifera are reported from the Silurian and Devonian of New South Wales, Victoria, and Tasmania.

IN 1964-5, we had the opportunity to collect from the Palaeozoic rocks of Victoria, New South Wales, and Tasmania, south-eastern Australia, in order to assess the stratigraphic occurrence and geographic distribution of arenaceous foraminifera. A preliminary report on the Permian foraminifera of Tasmania has been made (Conkin and Conkin 1965*a*). We were able, through the kindness of Dr. Irene Crespin and Dr. D. J. Belford of the Bureau of Mineral Resources, Geology, and Geophysics at Canberra to study the types of Dr. Crespin's (1961) Upper Devonian foraminifera from the Virgin Hills and Gogo Formations of the Fitzroy Basin, Western Australia. It was discovered that some of the forms would require revision in the light of work done on arenaceous foraminifera after the completion of Dr. Crespin's work. With these revisions made, the relationships between this important fauna of Crespin (1961) and similar faunas in the United States and Europe can be more clearly seen.

Past work. Crespin (1961, p. 397) summarized the record of Devonian foraminifera in Australia as follows:

In 1918 Chapman described and figured three genera and five species of what he considered to be foraminifera from thin sections of a limestone of Devonian age from the Nemingha area, Tamworth, northern New South Wales. However, Wood (1957) stated that these forms were 'oolite grains more or less affected by dolomitization and by mechanical distortion'. Parr (*in* Teichert and Talent 1958) reported poorly preserved arenaceous foraminifera from Devonian rocks in the Buchan area, east Gippsland, Victoria.

Chapman (1933) described two species of foraminifera from the Silurian of Victoria, '*Trochammina bursaria*' and '*Hemigordius lilydalensis*'; the former is perhaps conspecific with *Thuramminoides sphaeroidalis* Plummer 1945, which may not be a foraminiferan, but possibly a radiolarian or spore-like body (Conkin, Conkin, and Canis 1968); the latter is an indeterminate arenaceous foraminiferan and certainly not the calcareous *Hemigordius* or even a siliceous replacement of *Hemigordius*.

Crespin's (1961) fauna, the first important foraminiferal fauna from the Devonian of Australia, contains four genera and eight species as revised in the present paper.

[Palaeontology, Vol. 11, Part 4, 1968, pp. 601-9, pls. 114-17.]

Present work. Silurian and Devonian foraminifera were observed by us in the following states and stratigraphic horizons:

Tasmania, upper part of the Middle Devonian Point Hibbs Limestone at Point Hibbs: *Sorosphaeroidea* sp.

Victoria, east Gippsland, Devonian Pyramid Member of the Buchan Cave Limestone at Bindi: *Tolypammina* spp., *Sorosphaeroidea* sp., and *Hyperammina*? sp.

New South Wales, Yass-Taemas area, Devonian *Spirifer yassensis* beds: *Hyperammina* sp. and *Colonammina*? sp.

Victoria–New South Wales border area, Silurian Cowombat Formation at Cowombat Flat: *Hyperammina* sp., *Tolypammina* sp., and *Psammospaera*? sp.

The presence of these foraminifera in the Palaeozoic of Australia shows the need for further work on this group along the lines of Crespin (1958, 1961). We are in the process of describing these foraminifera from the Silurian and Devonian of Australia as well as making a detailed study of the magnificent arenaceous foraminiferal faunas from the Permian of Tasmania.

DISCUSSION OF GENERA

Saccammina Sars 1869. This genus consists of a simple agglutinated chamber with an aperture which may or may not have a short neck; as thus understood, *Saccammina* has been reported from Silurian to Recent.

Sorosphaeroidea Stewart and Lampe 1947 has a distinctive aperture which was not originally noticed by Stewart and Lampe or subsequently by Summerson (1958).

Oxinoxis Gutschick 1962, emended Conkin and Conkin 1964. The range of *Oxinoxis*, previously reported only from the United States, is upper Middle Devonian (middle and upper Hamiltonian) to Lower Mississippian (Kinderhookian and lower Osagean). Middle Devonian forms are almost exclusively single chambered and small. Upper Devonian forms are single to multiple chambered, and small to large. Kinderhookian and lower Osagean forms are generally much like the Upper Devonian, although there is in addition a distinct single chambered species of *Oxinoxis* in the Kinderhookian (Conkin, Conkin, and Canis 1968).

Tolypammina Rhumbler 1895. This attached genus ranges from Ordovician to Recent. Pre-Upper Devonian forms appear to wind or twist in a haphazard, disorganized manner, while some of the post-Middle Devonian forms wind, at least partially, in a more organized pattern. It is probable that the even more 'organized', but similar genus, *Ammonvertella* Cushman 1928, which apparently arose in the Kinderhookian, was derived from *Tolypammina*.

Hyperammina Brady 1878 is known from Ordovician to Recent. It is not present in Crespin's Upper Devonian fauna (1961), but occurs in the Silurian Cowombat Formation in the New South Wales–Victoria border area. The restricted generic definition of *Hyperammina* of Loeblich and Tappan (1964, p. C190) is not used. *Hyperammina* is employed in the sense of Brady 1878, as emended by Conkin (1954, 1961), and discussed by Conkin and Conkin (1965*b*, p. 211). It is basically a test with a free proloculus and

a free second chamber of more or less tubular shape, tapering and/or slightly constricted in some species. *Hyperanummina* has great potential as a tool in stratigraphic palaeontology within the Palaeozoic; a beginning along this line has been made within the Lower Mississippian of the United States (Conkin 1961).

Psanimosphaera Schulze 1875 consists of a simple agglutinated spherical or globular chamber with no obvious aperture. It has been reported from Ordovician to Recent.

AGE OF THE VIRGIN HILLS FORMATION BASED ON FORAMINIFERA

Crespin (1961) reported only two specimens from that portion of the Upper Devonian of Western Australia which may be referred to the Gogo Formation. Most of her specimens came from the overlying Upper Devonian Virgin Hills Formation.

Considered strictly in terms of the known stratigraphic ranges of foraminiferal genera included, the Virgin Hills Formation could be of late Middle Devonian, Late Devonian, or Early Mississippian (Kinderhookian) age. *Sorosphaeroidea*, previously thought by us to be restricted to beds older than Mississippian, has now been discovered in rare numbers in the Kinderhookian McCraney Limestone of north-eastern Missouri. *Oxinoxis* has not been found below the upper Middle Devonian, but it ranges into the lower Osagean.

On a specific level, however, *Tolypammina helina*, with a test consisting of an initially coiled portion and a final extended portion, is an 'organized' kind of *Tolypammina* which is post-Middle Devonian in its stratigraphic occurrence. The foraminiferal fauna of the Louisiana Limestone (Upper Devonian) from Missouri and Illinois is the oldest fauna from which this type of *Tolypammina* has been described (Conkin and Conkin 1964) in North America; a similar species is found in the Upper Devonian of Germany (Blumenstengel 1961). Thus, *T. helina* places the Virgin Hills Formation in the Upper Devonian or Lower Mississippian, rather than the Middle Devonian.

SYSTEMATIC PALAEOLOGY

The following observations are based on a study of Dr. Crespin's type specimens of Upper Devonian foraminifera at the Bureau of Mineral Resources, Geology and Geophysics, Canberra, A.C.T., Australia, and on a discussion of the fauna with Dr. Crespin. Text-fig. 1 is based on drawings made at that time and on photomicrographs taken subsequently and forwarded to us by Dr. D. J. Belford. Type numbers refer to Commonwealth Palaeontological Collection (CPC), and holotype and paratype designations are the original ones of Crespin (1961).

Family SACCAMMINIDAE

Genus SACCAMMINA M.Sars 1869

Saccammina glenisteri Crespin 1961

Plate 116, figs. 1-7.

1961 *Saccammina glenisteri* Crespin, pp. 401, 402, pl. 65, figs. 3-7.

The holotype (CPC 401; Pl. 116, figs. 1-3) has slit-like? aperture as figured by Crespin, and a few holes of secondary nature; the test, one grain thick, is composed of coarse grains of quartz in a fine-grained matrix; there is no evidence of attachment.

Paratype A (CPC 402; Pl. 116, figs. 6, 7) has a coarse-grained, subglobular test with an elongate, lunate aperture; there is no evidence of attachment.

Paratype B (CPC 403) has a rounded aperture; there is no evidence of attachment.

Paratype C (CPC 404; Pl. 116, figs. 4, 5) has a knob-like structure on the inside of the broken test which is like the structure found on the interior of the test and just below the aperture in *Sorosphaeroidea*, but which in this case may be secondarily formed.

Paratype D (CPC 405) consists of two globular tests attached to a *Tolypammina* fragment and composed of coarse grains of quartz; the apertures are indistinct, and the tests are smaller than the other types of this species; this specimen came from the Gogo Formation which underlies the Virgin Hills Formation from which the other specimens came. The identity of Paratype D is not certain since the tests are attached on a small surface and are thus not completely free.

Genus *SOROSPHAEROIDEA* Stewart and Lampe 1947

Sorosphaeroidea adhaerens (Crespin) 1961

Plate 116, figs. 8–11; text-fig. 1c

1961 *Sorosphaera adhaerens* Crespin, pp. 403, 404, pl. 66, figs. 1–5.

The holotype (CPC 406; Pl. 116, figs. 8, 9) consists of chambers which are attached to a *Tolypammina* fragment and the nature of the surface of attachment on the test (whether covered with a floor or open), is not known. Its reference to *Sorosphaeroidea* is uncertain, but probably correct.

Paratype A (CPC 407) consists of several chambers which are indistinct on one side, and attachment areas are somewhat obscure.

Paratype B (CPC 408; Pl. 116, figs. 10, 11; text-fig. 1c) possesses broad, flattened attachment scars (not originally figured), which are somewhat finer grained than the upper side of test; there is a definite aperture on the upper, unattached side of each chamber. A fragment of a *Tolypammina* is attached to the specimen.

Paratype C (CPC 409) is attached to a *Tolypammina* fragment, but the attached surface is not visible; an aperture is present on the upper side.

Paratype D (CPC 410) has an aperture on the upper unattached side; the attached side is not visible as it is fastened to a fragment of *Tolypammina*.

Remarks. Paratype B is definitely referable to *Sorosphaeroidea*; the other types have the attachment surface hidden, or it is obscure (Paratype A), but they probably belong to this genus also. We place this species in *Sorosphaeroidea* because of the large areas of attachment, and because the apertures generally are like those which we have found in the original types of *Sorosphaeroidea* of Stewart and Lampe; the aperture appears inverted, as if pushed through from the outside.

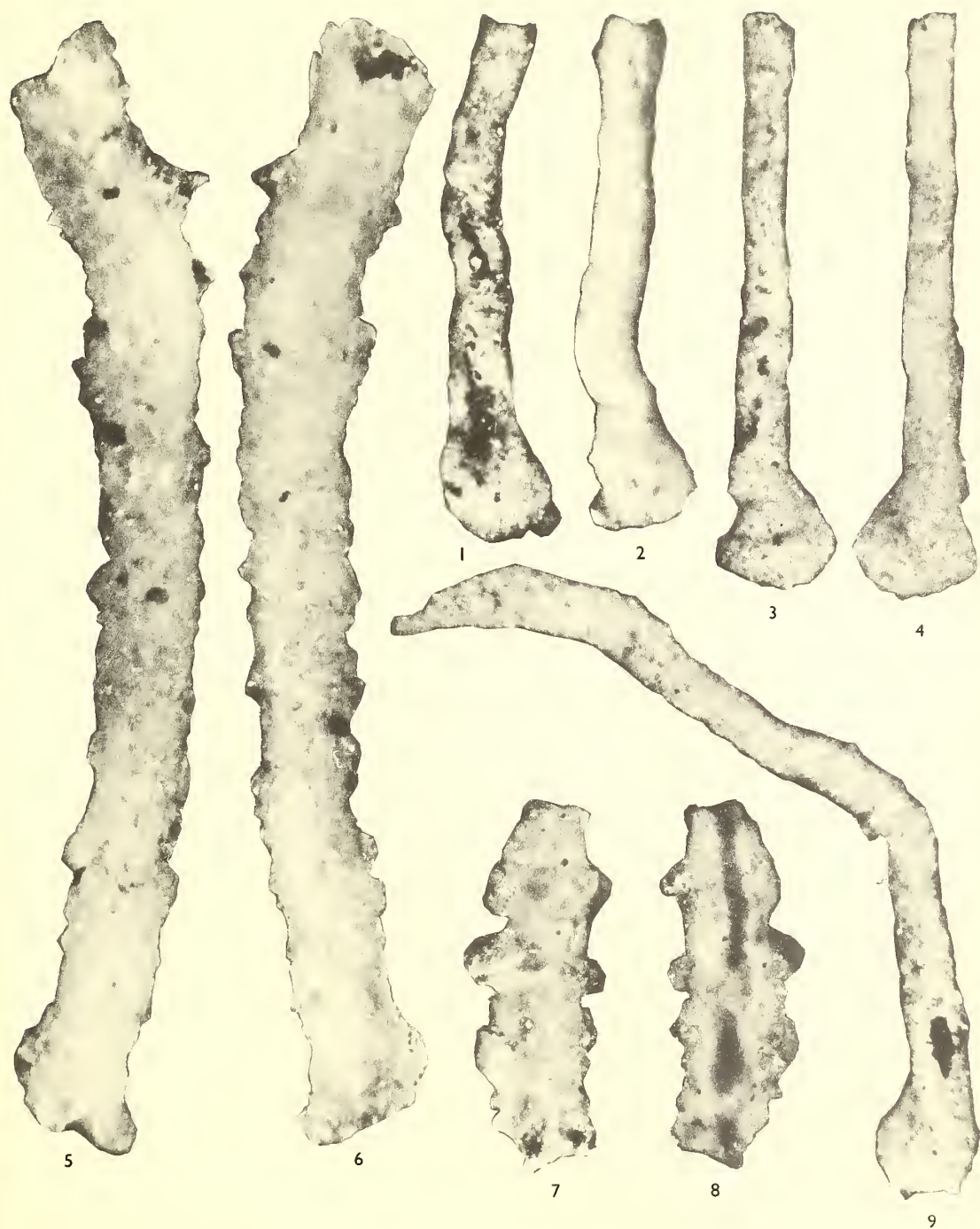
EXPLANATION OF PLATE 114

Figs. 1–4, 9. *Tolypammina devoniana* (Crespin) 1961. 1, Paratype A; basal, attached side showing rather large attachment scars, smoothly polished along the edges. 2, Paratype D, top view. 3, Side view of holotype showing attachment scar on the proloculus and small areas of attachment along the length of the second chamber. 4, Top view of holotype showing slight notch on proloculus. 9, Paratype E, top view showing break in test.

Figs. 5, 6. *Tolypammina*? sp. 5, Plesiotype (holotype of '*Rhabdammina virgata*' Crespin 1961), showing fragmentary nature and coarse-grained texture of the test. 6, Reverse side of same specimen; proloculus and aperture are not preserved.

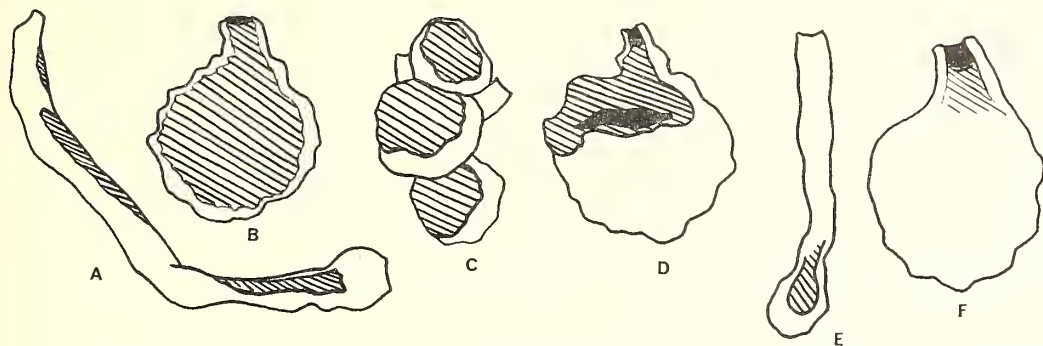
Figs. 7, 8. *Tolypammina* sp. 7, Plesiotype of '*Marsipella* sp.', Crespin 1961; top view of hemitubular fragment showing rough and coarse-grained test. 8, Basal view of same specimen showing attached lower surface.

All figures approximately $\times 105$.



CONKIN and CONKIN, Upper Devonian arenaceous foraminifera

The Middle Devonian forms of *Sorosphaeroidea* described by Stewart and Lampe (1947) and Summerson (1958) are more regularly shaped and arranged than the present forms.



TEXT-FIG. 1. Schematic drawings of attached sides of *Tolypammina devoniana* (A, E), *Oxinoxis ampullacea* (B, D, F), and *Sorosphaeroidea adhaerens* (C). All figures approximately $\times 50$. Hatched areas are flattened surfaces of attachment. Black arcs indicate openings into test. White areas are unattached portions of test.

Family REOPHACIDAE

Genus OXINOXIS Gutschick 1962, emend. Conkin and Conkin 1964

Oxinoxis ampullacea (Crespin) 1961

Plate 117, figs. 1–11; text-fig. 1B, D, F

1961 *Lagenammina ampullacea* Crespin, pp. 404, 405, pl. 66, figs. 6–8.

1961 *Colonammina imparilis* Crespin, pp. 405, 406, pl. 65, figs. 10–13.

1961 *Protonina* sp., Crespin, p. 404, pl. 65, fig. 8.

The holotype of '*Lagenammina*' *ampullacea* (CPC 412; Pl. 117, figs. 1–3) has a faint flattened attachment scar at the base, but otherwise the chamber is nearly spherical with a small apertural neck.

Paratype A of '*Lagenammina*' *ampullacea* (CPC 413; Pl. 117, fig. 11) is slightly flattened on the basal side, with a somewhat finer-grained texture there than on the upper side, but with some larger quartz grains studded on it; there is a small apertural neck.

Paratype B of '*Lagenammina*' *ampullacea* (CPC 414) has a rather prominent apertural neck with the basal side flattened; there is also a small, slightly roughened attachment area at the base of the chamber.

The holotype of '*Colonammina*' *imparilis*' (CPC 415; Pl. 117, figs. 4–6; text-fig. 1D) consists of a nearly spherical chamber with a prominent wedge-shaped attachment scar forming a re-entrant into the test below the neck; the prominent apertural neck is hemitubular with the basal surface flattened and attached.

Paratype A of '*Colonammina*' *imparilis*' (CPC 416) has a flattened attachment scar on the basal side which is finer grained than the unattached, upper, convex side; the prominent tubular apertural neck has no attachment scar.

Paratype B of '*Colonammina*' *imparilis*' (CPC 417; Pl. 117, figs. 7, 8; text-fig. 1B) has a large basal attachment scar which is fine grained and has a polished lustre; the apertural neck is only partly attached on its basal side; the convex upper unattached side of the test is coarse grained.

Paratype C of '*Colonammina*' *imparilis*' (CPC 418) is an obscure specimen; the apertural neck figured by Crespin (1961, pl. 65, fig. 13) appears to be part of another specimen and thus foreign to paratype C; the base of the test is flattened and has a prominent fine-grained attachment scar with a polished lustre; this specimen is not typical of the species, but does apparently belong to *O. ampullacea*.

'*Proteonina* sp.' (CPC 411; Pl. 117, figs. 9, 10; text-fig. 1F) is a compressed test with holes and depressions in the wall left after calcareous grains were leached out; the apertural neck is partly hemitubular and has a small attachment scar on the basal side at the apertural end, and after which the neck is tubular adjacent to the chamber, which is itself unattached; this specimen is from the Gogo Formation.

Remarks. The presence of an attachment scar on the chamber of the test and/or on the hemitubular to tubular apertural neck serves to place these specimens in *Oxinoxis*.

O. ampullacea differs from the type species *O. ligula* (Gutschick, Weiner, and Young 1961), which occurs in the Upper Devonian and Lower Mississippian in the United States, in having a more coarse-grained test and in being nearly twice as large as the single-chambered, more solidly-walled forms of *O. ligula*.

Family AMMODISCIDAE

Genus TOLYPAMMINA Rhumbler 1895

Tolypammina devoniana (Crespin) 1961

Plate 114, figs. 1-4, 9; text-figs. 1A, E

1961 *Hyperammina devoniana* Crespin, pp. 406, 407, pl. 64, figs. 1-6.

The holotype (CPC 419; Pl. 114, figs. 3, 4) has a proloculus which is asymmetrical, shaped rather like the head of a golf club, owing to a notch-like attachment scar on its basal surface where it joins the second chamber; this basal side of the proloculus is partially attached and there are attachment scars at irregular intervals and distances along the elongate second chamber.

EXPLANATION OF PLATE 115

Figs. 1-4. *Tolypammina helina* Crespin 1961. 1, Holotype, basal flattened and attached side of hemitubular test. 2, Top view of holotype showing proloculus, $2\frac{1}{2}$ planispiral whorls, and extended portion. 3, Paratype A, basal view showing the completely attached hemitubular test, and an early unsuccessful attempt to uncoil (after $1\frac{1}{2}$ planispiral whorls) with return to planispiral coiling for $1\frac{1}{4}$ whorls more before finally uncoiling. 4, Top view of paratype A, showing proloculus, rather obscure whorls, and extended portion.

FIGS. 5-8. *Tolypammina nexuosa* Crespin 1961. 5, Paratype B of *Tolypammina 'helina'*, top view. 6, Basal view of same specimen showing complete attachment of hemitubular test; no proloculus preserved. 7, Holotype of *Tolypammina nexuosa*, top view. 8, Basal view of holotype, showing attached side of test.

All figures approximately $\times 105$.

EXPLANATION OF PLATE 116

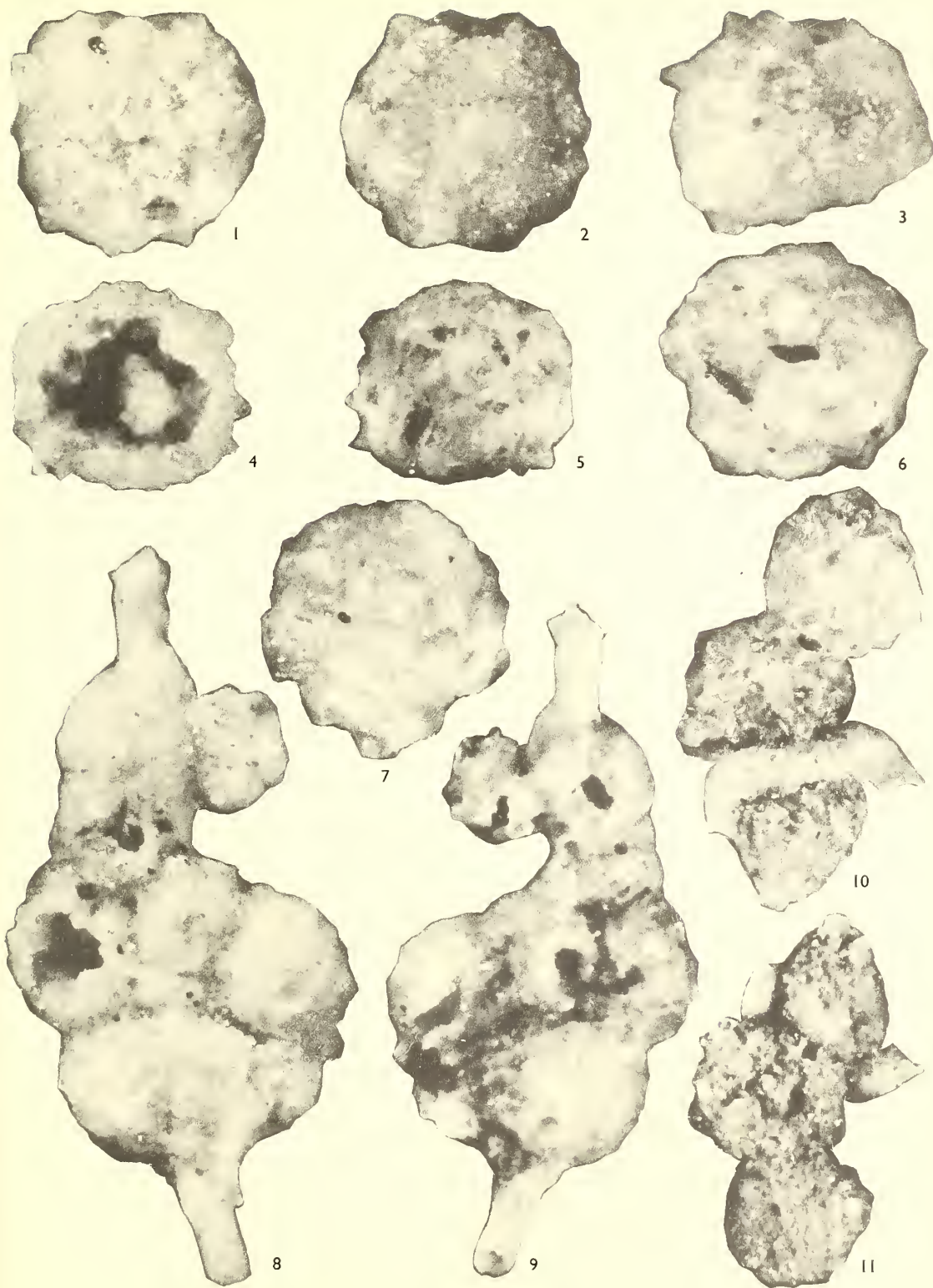
Figs. 1-7. *Saccammina glenisteri* Crespin 1961. 1, Holotype, upper apertural view, showing slit-like aperture in centre of test. 2, Basal view of holotype. 3, Side view of holotype. 4, Paratype C, broken test showing knob-like structure underneath the aperture on the interior of the test. 5, Exterior view of paratype C showing aperture in the centre of the test. 6, Paratype A, upper apertural view of test showing slit-like aperture in the centre of the test. 7, Basal view of paratype A.

Figs. 8-11. *Sorosphaeroidea adhaerens* (Crespin) 1961. 8, Holotype, view of aggregate of chambers shown by Crespin (1961, pl. 66, fig. 1) showing attachment to foreign body. 9, Reverse side of specimen. 10, Paratype B, upper unattached surface of test showing aperture piercing middle chamber and an attached fragment of *Tolypammina*. 11, Basal view of paratype B showing flattened chambers on attached side of test.

All figures approximately $\times 105$.



CONKIN and CONKIN, Upper Devonian arenaceous foraminifera



Paratype A (CPC 420; Pl. 114, fig. 1) is like the holotype; a prominent attachment scar beginning about midway along the proloculus and smoothly polished along the edges, extends approximately half the length of the test.

Paratype B (CPC 421) consists of a nearly symmetrical test which is, however, slightly flattened with an attachment scar on the basal side; the test is somewhat longer than originally shown.

Paratype C (CPC 422) is an asymmetrical test with a slightly flattened attachment scar on the basal side.

Paratype D (CPC 423; Pl. 114, fig. 2; text-fig. 1E) is an asymmetrical and crooked test; the proloculus has a large notched attachment scar which extends a short distance along the second chamber; the edges of the scar are polished and the scar itself has a fine-grained texture.

Paratype E (CPC 424; Pl. 114, fig. 9; text-fig. 1A) is a quite crooked test with the second chamber hemitubular over most of its length owing to attachment scars on one side; short intervals of the second chamber are tubular with no attachment along these portions; the attachment scar extends only slightly on the proloculus.

Remarks. *T. devoniana* is a good example of the genus even though the attachment scars are only slightly developed in some specimens. *Tolypammina* is attached at intervals along or throughout, the length of the second chamber, while the proloculus may be free, attached, or partially attached as in the present species. The hemitubular nature of the second chamber is characteristically developed to some degree on the attached portions, but this is not so in *Hyperammina*, which is entirely free.

T. devoniana differs from a similar species, *T. bulbosa* (Gutschick and Treckman 1959), which occurs in the Upper Devonian and Lower Mississippian of the United States, in having a more irregularly shaped and partially attached proloculus, while the proloculus of *T. bulbosa* is free and quite spherical.

Tolypammina helina Crespin 1961

Plate 115, figs. 1–4

1961 *Tolypammina helina* Crespin (*in part*), p. 407, pl. 67, figs. 1–4.

The holotype (CPC 425; pl. 115, figs. 1, 2) has an attached proloculus and a hemitubular second chamber which is flattened all along the basal attached side and is only partly floored; whorls are all roughly in the same plane; the upper, unattached side is somewhat obscure and was shown slightly incorrectly in the original drawing; the present figure (Pl. 115, fig. 2) shows the nature of the whorls on this dorsal side.

Paratype A (CPC 484; Pl. 115, figs. 3, 4) is a completely attached test which is flattened on the basal side, with the second chamber hemitubular throughout and only partly floored; the whorls are roughly in the same plane.

Remarks. *T. helina* is remarkably similar to *T. gersterensis* Conkin and Conkin 1964, which occurs in the Upper Devonian and Lower Mississippian of the United States. A similar species, in part at least, is *T. irregularis* Blumenstengel 1961, from the Upper Devonian and Lower Carboniferous of Germany; the exact relationships between these species are not certain.

Tolypammina nexuosa Crespin 1961

Plate 115, figs. 5–8

1961 *Tolypammina nexuosa* Crespin, pp. 407, 408, pl. 67, figs. 6–8.

1961 *Tolypammina helina* Crespin (*in part*), p. 407, pl. 67, fig. 5.

The holotype (CPC 486; Pl. 115, figs. 7, 8) displays an irregular pattern of twisting and winding.

Paratype A (CPC 487) possesses a flat, attached, basal side; no proloculus is visible; the rounded hump on the specimen is not the proloculus, but merely a bend in the hemitubular second chamber.

Paratype B (CPC 488) has a hemitubular test which is flat and attached on the basal side; no proloculus is present.

Paratype B of *Tolypammina* 'helina' (CPC 485; Pl. 115, figs. 5, 6) probably belongs to *T. nexnosa* for it does not possess a planispiral portion; the basal side is flat and the second chamber is hemitubular.

Remarks. This species is of doubtful status, for a proloculus should be seen in order to erect a species and to make specific identification in the genus *Tolypammina*; the early relationship of the second chamber to the proloculus is usually distinctive in a given species.

Tolypammina sp.

Plate 114, figs. 7, 8

1961 *Marsipella* sp., Crespin, p. 401, pl. 65, fig. 9.

This specimen (CPC 400; Pl. 114, figs. 7, 8) consists of a broken test with no proloculus preserved; the test is hemitubular and attached, with the attached side open, without a floor; upper unattached side is of coarse and clear quartz grains.

Remarks. This specimen clearly belongs to *Tolypammina*, even though it is a fragment, for it is hemitubular and attached.

Tolypammina? sp.

Plate 114, figs. 5, 6

1961 *Rhabdammina virgata* Crespin, pp. 400, 401, pl. 64, figs. 7-10; pl. 65, figs. 1, 2.

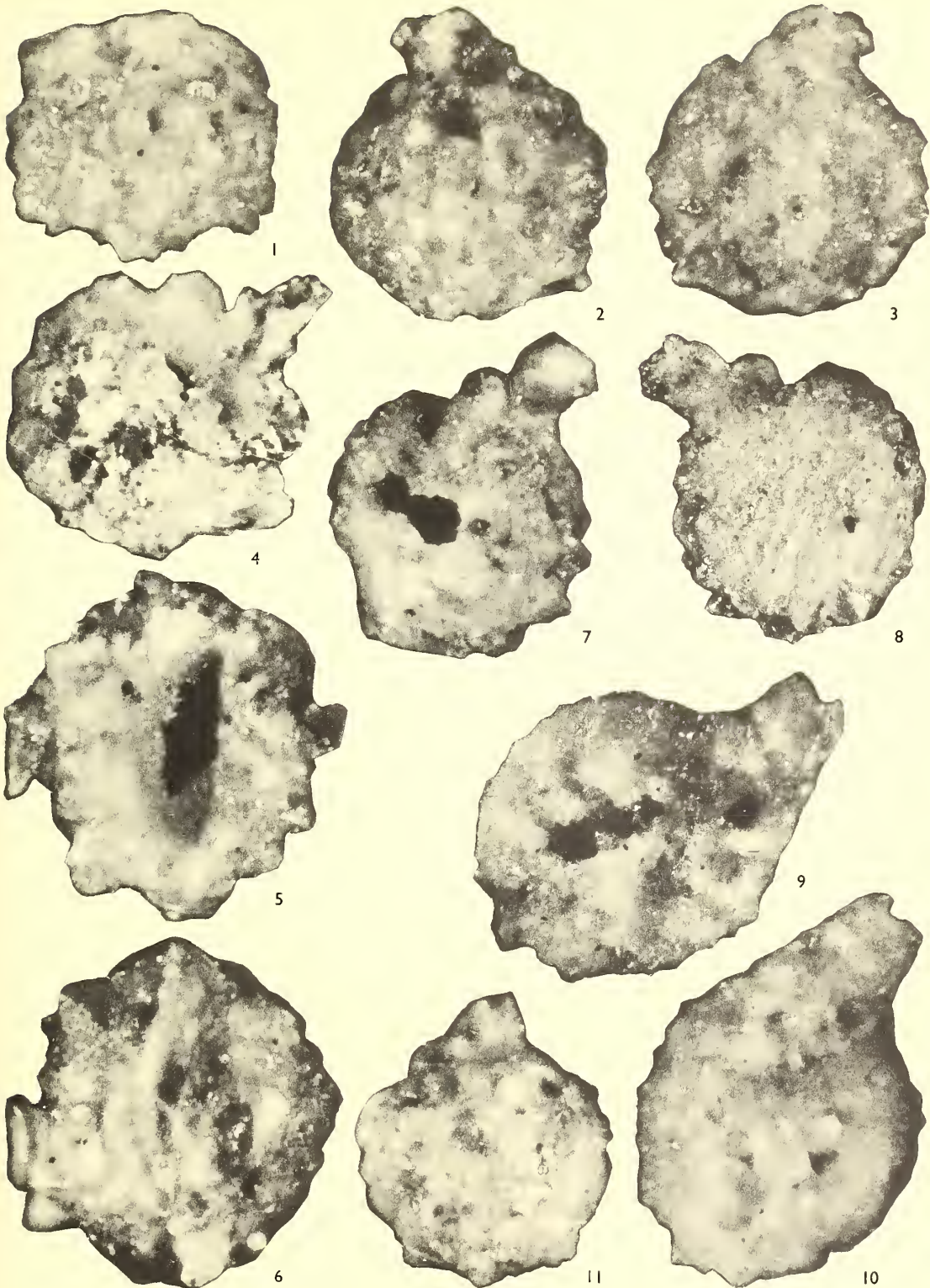
The holotype (CPC 394; Pl. 114, figs. 5, 6) consists of a test which is broken at both ends so that the nature of the proloculus and aperture is not known; this fragment is tubular, with no evidence of attachment noted, but the test is only partly preserved; the test is composed of medium to coarse quartz grains. Although the evidence for positive generic assignment is not present in this specimen, we prefer to regard this specimen as belonging to *Tolypammina* rather than *Rhabdammina*.

Paratype A (CPC 395) is a limonitic cast of an orange colour; the test is broken at both ends and is curved; no proloculus is present.

EXPLANATION OF PLATE 117

Figs. 1-11. *Oxinoxis ampullacea* (Crespin), 1961. 1, Holotype of '*Lagenammina*' *ampullacea*, side view. 2, Upper surface of same specimen. 3, Basal attached side of same specimen. 4, Holotype of '*Colonammina imparilis*' Crespin; oblique view of basal attachment and upper surface showing hemitubular apertural neck and partially obscured wedge-shaped attachment scar. 5, Basal attached surface of same specimen showing attachment scar. 6, Upper surface of coarse-grained test, same specimen, showing a few coarser quartz sand grains incorporated in the test. 7, Paratype B of '*Colonammina imparilis*', upper convex surface of test showing holes in the wall, not apertural, due to breakage. 8, Basal attached surface of same specimen showing large attachment scar. 9, Plesiotype of '*Proteonina* sp.', Crespin 1961, basal attached and pitted surface of test. 10, Upper pitted surface of test, same specimen. 11, Paratype A of '*Lagenammina*' *ampullacea* Crespin 1961, upper surface.

All figures approximately $\times 105$.



CONKIN and CONKIN, Upper Devonian arenaceous foraminifera

Paratype B (CPC 396) is a bent and curving test, broken at both ends, with no proloculus or aperture; tube is composed of coarse-grained quartz.

Paratype C (CPC 397) is broken at both ends and is curved; no proloculus is preserved.

Paratype D (CPC 398) consists of an irregularly coiled test, broken at both ends; no proloculus is preserved.

Paratype E (CPC 399) is broken at both ends with no proloculus preserved; the test is red-orange in colour and is composed of quartz sand grains.

Remarks. These specimens appear to be fragments of free portions of *Tolypammina*, but specific identification is impossible.

Acknowledgements. We are grateful to: Dr. Irene Crespin for her kind permission to revise these foraminifera; Dr. D. J. Belford for photographing the specimens; Dr. John Talent, who led us to the fossiliferous outcrops of the Silurian Cowombat Formation in Gippsland and southern New South Wales; Mr. Edmund Gill, who facilitated examination of type specimens in the Victoria Museum, Melbourne, and Dr. K. S. W. Campbell for guiding us in a study of the Yass-Taemas area, New South Wales.

This work was made possible by a Fulbright Senior Research Fellowship to the University of Tasmania and sabbatical leave from the University of Louisville in 1964–5.

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JAMES E. CONKIN
Department of Geology
University of Louisville
Louisville, Kentucky 40208
U.S.A.

BARBARA M. CONKIN
Jefferson Community College
University of Kentucky
Louisville, Kentucky 40202
U.S.A.

A NEW MEDUSOID (?) FROM THE SILURIAN OF ENGLAND

by ISLES STRACHAN

ABSTRACT. *Duodecimedusina palmeri* sp. nov. is described from the Upper Llandovery of the Malverns and West Midlands. This extends the stratigraphic range of the genus previously described from the Carboniferous and Lower Devonian. It is also the first record from Europe.

ONE of the specimens described here was picked up some years ago on a student field excursion to the Lickey Hills, just south of Birmingham. Like so many interesting specimens it was a loose block so that there is no direct evidence of which way up the specimen was, or more important, from which geological horizon it came, both Cambrian and Lower Silurian being exposed in the quarry. In June 1967, a similar specimen (for which the stratigraphic horizon is more precise) was collected by Mr. K. F. Palmer on a student trip to the Malverns. The confirmation of geological age and morphological features make recording of the specimens more important since the range of the genus is considerably extended in time and space.

Genus DUODECIMEDUSINA King

This genus was proposed by King (1955) for three species, *D. typica*, *D. wycherleyi*, and *D. ulrichi*. The first two of these, known from a single specimen each, come from Upper Carboniferous of Kansas, and the third species, also from a single specimen, is from the Lower Devonian of Bolivia. Avnimelech (1966) has recently described a fourth species, *D. aegyptica* from the Lower Carboniferous of Egypt, again from a single specimen. The present specimens therefore extend the range of the genus down to the Lower Silurian as well as being the first record from Europe.

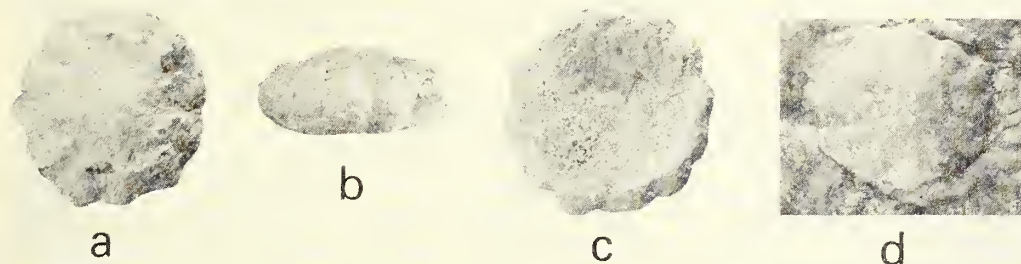
Harrington and Moore (1956) classified *Duodecimedusina* amongst the 'Medusae Incertae Sedis' but Avnimelech has proposed transferring the genus to the Proto-medusae on the grounds of similarity to *Brooksella* which forms the whole class. The latter genus, however, frequently shows supplementary lobes on the sub-umbrellar surface which are not found in the Egyptian and British specimens. The American specimens are all attached to a 'pedestal' so that the sub-umbrellar surface cannot be seen. The general category of 'Medusae Incertae Sedis' therefore seems to me to be a better resting place for *Duodecimedusina* for the present.

Duodecimedusina palmeri sp. nov.

Material. Holotype, BU 302, from base of Upper Llandovery, Gullet Quarry, Malverns, in a slightly micaceous siltstone, way-up not known. Paratype, BU 303, probably from Rubery Sandstone (Upper Llandovery), Rubery Quarry, Leach Green Lane, Birmingham, in a medium to coarse sandstone.

Description. Body roughly circular, 16–19 mm. in diameter. There is a central raised

area, rather poorly defined, occupying about half of the diameter, surrounded by twelve lobes. The lobes are distinct at the periphery, measuring about 3 mm. across, but merge centrally into the more raised area. The undersurface is poorly preserved in the holotype and not seen on the paratype.



TEXT-FIG. 1. *a, b, c.* Holotype, BU 302, exumbrellar, side, and subumbrellar views. *d.* Paratype, BU 303, exumbrellar view. All $\times 1\frac{1}{2}$.

Discussion. *D. palmeri* is similar to *D. typica* King in the poorly delimited area of the exumbrellar surface but is little more than half its size. *D. wycherleyi* King is even smaller (10–11 mm. in diameter) but has a central depression, which is also found in the Lower Devonian, *D. ulrichi* King. *D. aegyptica* Avnimelech is similar in size to *D. palmeri* but is much more convex in lateral view and has more clearly marked off lobes.

Since the above was written, Dr. Goldring has sent me another specimen from the Gullet Quarry. This specimen (Reading Univ. Geol. Dept. no. 14601) was collected as a loose specimen by Mr. D. C. Smith while mapping the area. It is somewhat larger (about 28 mm. in diameter) and the lobes show weak, but fairly constant, concentric bands, a feature not reported on any other of the species.

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ISLES STRACHAN
 Geology Department
 University of Birmingham
 P.O. Box 363
 Birmingham, 15

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THE ATRYPIDINE BRACHIOPOD *DAYIA* *NAVICULA* (J. DE C. SOWERBY)

by E. V. TUCKER

ABSTRACT. The atrypidine brachiopod *Dayia navicula* (J. de C. Sowerby) is described and a neotype is designated. The musculature is reinterpreted and shown to differ from previous interpretations. Comparisons are made between *Dayia navicula* s. str. and other forms referred to the species. Between the Ludlow and the Lower Devonian the shells increase in size and incurvature of the umbo becomes less marked.

PRIOR to 1881 the brachiopod now designated *Dayia navicula* rested uneasily in palaeontological works first under the style of *Terebratula navicula* and later *Rhynchonella? navicula*. M'Coy in 1846 anticipated in part the probable relationship between this form and the atrypids when he referred it to *Atrypa navicula*. In 1881 Davidson, studying material skilfully prepared by the Revd. N. Glass, recognized the distinctiveness of the brachidium and erected the new genus *Dayia*. Since then material referred to the species *D. navicula* has received attention especially in the hands of Kozłowski (1929, p. 179) and Alexander (1947). The latter undertook a morphological study of the characteristic British form but her conclusions contain certain misconstructions.

In stratigraphy, *Dayia navicula* has been widely used as an index of Ludlovian rocks, particularly for the Leintwardine Beds (formerly the *Dayia* or Mocktree Shales of Elles and Slater (1906)) which underlie the Upper Ludlow or Whitcliffe Beds. Straw (1937), however, noted its presence in rocks ranging from the *nilssoni* zone into the base of the Upper Ludlow at Builth. This extended range was re-emphasized by Earp (1938) and Shirley (1939 and 1952) for other parts of Wales and the Welsh Borderland. Davidson (1869, p. 191) in the monograph of Silurian brachiopods records Wenlock occurrences given in Murchison's 'Siluria' but only the general locality of Builth is mentioned.

A similar stratigraphical range has been suggested in continental Europe. Barrande (1879) records the species from the Upper Ordovician of Bohemia but this claim needs re-examination. In Scandinavia, Lower Ludlow forms, although smaller than the typical *Dayia navicula*, closely resemble certain British Elton Bed (Lower Ludlow) forms. Kozłowski's description (1929, p. 179) and illustrations of Podolian specimens from the Marnes de Dźwinogród, now believed by Jaeger (1965) and others to be post-Ludlovian and possibly Gedinnian in age, indicate close agreement with the characteristic British form. The existence of other sub-species, or at least variants of *Dayia navicula*, is suggested, however, by the work of Bouček (1940) and Shirley (1962). Shirley emphasizes the differences between varieties from the Schistes de Liévin and the Köbbinghauser Schichten of the Artois basin and Westphalia respectively, which have previously been referred to as *Dayia navicula*, and the characteristic British forms; a view endorsed by the present writer. This misidentification and the usage of *Dayia navicula* as a Ludlovian index fossil is partly responsible for the discordant views which have been expressed on the correlation of French-Rhenish and British successions.

In her account, Alexander referred (1947, p. 305) to a specimen in the Geological Survey collection as holotype. This specimen does not match Sowerby's illustration in Murchison's *Silurian System* (1839, pl. 5, fig. 17) however, differing in size, detail of ornamentation, nature of ventral umbo, and in its geographical location. Search elsewhere has failed to reveal the type specimens and they are presumed to have been lost. To assist future comparison a neotype for *Dayia navicula* is designated here, the morphology is re-described, the musculature reinterpreted and some aspects of variation in the genus are outlined.

The material on which the study is based has been collected by the writer, chiefly from the Leintwardine Beds of Downton Gorge (Herefordshire) and various Silurian inliers in the Welsh Borderland, particularly those of Woolhope and Usk, and from the Elton Beds and Whitcliffe Beds. These personal collections were supplemented by collections housed in the Geological Survey Museum (GSM) and Mrs. Alexander's collections of silicified specimens in the Sedgwick Museum, Cambridge (SM). (Manuscript notes of Alexander suggest that this collection was made near Greenway Cross (Nat. Grid. SO/461 827), although repeated visits to the same locality by the present writer have revealed few specimens of *Dayia navicula*. The fauna indicates a Lower Leintwardine age for the beds.) The source of foreign material is indicated in the appropriate section.

SYSTEMATIC DESCRIPTION

Superfamily DAYIACEA Waagen 1883

Family DAYIIDAE Waagen 1883

Subfamily DAYIINAE Waagen 1883

Genus DAYIA Davidson 1881

Type species. Terebratula navicula (J. de C. Sowerby) 1839.

Diagnosis. Small, strongly inequivalve, pedicle valve larger; hinge line gently curved; shell generally elongated medially but sometimes spherical. Brachial valve with sulcus expanding to one-third of shell width at anterior margin; weakly inflated laterally. Pedicle valve highly arched transversely, smoothly curved medially. Umbo normally incurved. Lateral commissure dorsally curved, anterior commissure sulcate. Surface ornamentation of very fine costae and weak growth-lines, indistinct.

Spire directed towards sides of pedicle valve but contained within the first coil. In the pedicle valve a platform of secondary callus supported the diductor muscles. Muscle fields deeply impressed, of chevron form. Adductor scars ill-defined. Prominent median septum in the brachial valve extends to three quarters valve length and separates well-developed adductor muscle fields. A septalium divides a subdued cardinal plate at the centre of the hinge-line.

Range. Silurian (Ludlovian, possibly Wenlock) to Devonian (Gedinnian). *Dayia* has been recorded from many Western European countries along a belt from the Dingle peninsula in south-west Ireland to Podolia in the U.S.S.R., and from Scandinavia. It is not known from extra-European areas.

Discussion. The pre-Ludlovian records of *Dayia* require re-investigation. *Dayia cynbula* (Davidson) has been recorded from the Caradoc Beds of Hendre Wen (North Wales) and from the Drummuck Group (Ashgillian) near Girvan. Reed (1917) described a variant '*girvanensis*' associated with it near Girvan. Externally there are many

similarities between these forms and *Dayia navicula*. The musculature of the pedicle valve differs in detail however and the teeth are more prominent. Dental plates, observed by Davidson, are lacking in *Dayia*. The nature of the brachidium of *Dayia cymbula* is not known.

Dayia navicula (J. de C. Sowerby)

Plates 118–21

- 1839 *Terebratulina navicula* Sowerby, p. 611, pl. v, fig. 17.
- 1846 *Atrypa navicula* (Sowerby); M'Coy, p. 40.
- 1848 *Hypothyris navicula* (Sowerby); Phillips, p. 281.
- 1852 *Hemithyris navicula* (Sowerby); M'Coy, p. 204.
- 1859 *Rhynchonella? navicula* (Sowerby); Lindström, p. 366.
- 1869 *Rhynchonella? navicula* (Sowerby); Davidson, p. 191.
- 1881 *Dayia navicula* (Sowerby); Davidson, p. 291.

Neotype. A specimen collected by the writer and deposited in the Geological Survey Museum (GSM 103291) is selected as neotype (Pl. 118, fig. 2). Sowerby's type locality is vaguely defined. The neotype is from the Lower Leintwardine Beds of Downton Gorge, Herefordshire (Nat. Grid SO/431 733) approximately 55 ft. above the base.

Occurrence. *Dayia navicula* is present throughout the Leintwardine Beds of the Welsh Borderland, being most common in western areas. It extends upwards into the Lower Whitcliffe Beds, especially in adjacent parts of Wales. Closely allied forms also occur in the Elton Beds of these areas and at similar levels in Scandinavia whilst other variants range upwards into Lower Devonian rocks of central Europe.

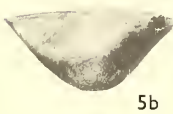
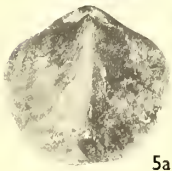
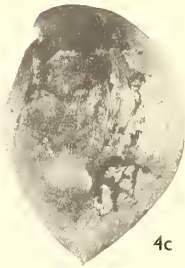
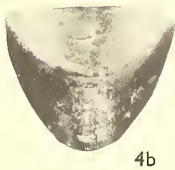
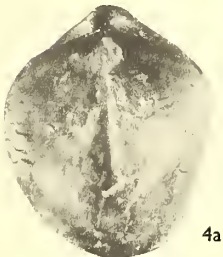
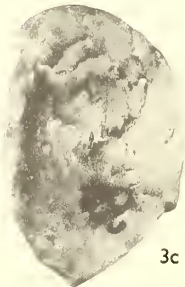
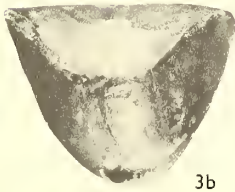
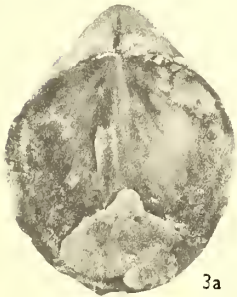
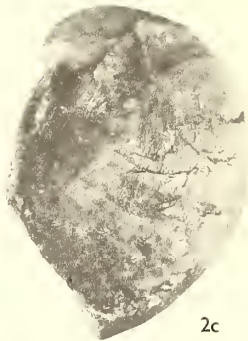
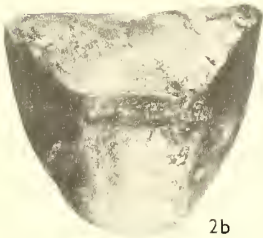
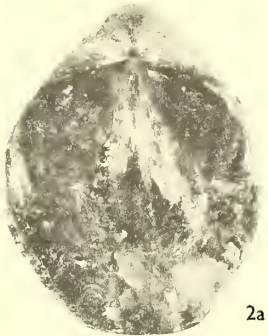
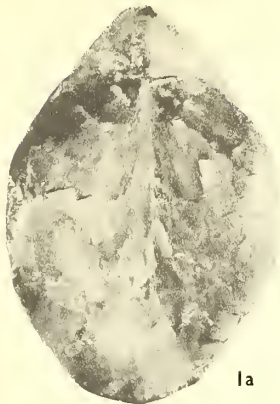
Dimensions of neotype. Length 10.4 mm., width 8.0 mm., thickness 7.2 mm.

Diagnosis. As for the genus. The umbo characteristically is gibbous and rests upon the brachial valve, effectively sealing the foramen. The diductor muscle platform is prominent in the pedicle valve and the chevron scars occupy much of the shell width.

Description. Considerable shape variation can be recognized. Ontogenetic studies demonstrate a progressive relative increase in elongation with age. (Pl. 118, figs. 1–5). This is generally accompanied by a deepening of the sulcus in the brachial valve and accentuation of umbonal incurvature in the pedicle valve. This incurvature ultimately caused pedicle atrophy during maturity (Tucker 1965). In juvenile growth stages the sulcus remains shallow and smoothly curved transversely. It becomes steeper sided in mature forms, where there is an equal division between forms with a deep, flat-bottomed sulcus and those more sharply angular. Variation in mature shells is expressed also by differences in degree of elongation and degree of incurvature of the ventral umbo. Most shells have a pronounced elongation (the width to length ratio exceeding 1:1.2) but

EXPLANATION OF PLATE 118

Figs. 1–5. *Dayia navicula* (J. de C. Sowerby). All un-numbered specimens in author's collection. Lower Leintwardine Beds, Downton Gorge, Herefordshire. National Grid: SO/431 733. Dorsal, anterior, and lateral views of five growth stages. Fig. 2 is designated neotype (GSM 103291) (all $\times 4$).



some retain more squarish outlines. All mature shells have a strongly incurved umbo but this is accompanied by excessive elevation of the posterior part of the ventral valve in some specimens, producing an acute transverse arch which accentuates elongation of the shell.

Dentition. The teeth diverge at an angle of less than 160° . Their length is almost one-quarter the shell width. They are most prominent posteromedially, hence articulation is best defined towards the centre-line where the inward and partly downward facing edge of each tooth locks into a laterally opening notch within the sockets (see text-fig. 1g). Thickening of the inner socket-ridge beneath, and to a lesser extent above, the socket is accompanied by a swelling into the visceral cavity, intensifying the socket and assisting articulation. The stages of development of the inner socket ridge are demonstrated by the pattern of growth lines shown in text-fig. 3d.

The crenulations on the dorsal surface of the teeth referred to by Alexander (1947, p. 307), are rarely apparent although similar features, lying on the inner face, have been observed on one silicified mould in her collection. There is no clear indication of these features in the micro-structure of other, calcareous, shells.

Lophophore supports. These comprise crura and laterally directed spires united by a comparatively simple jugum (see text-fig. 1).

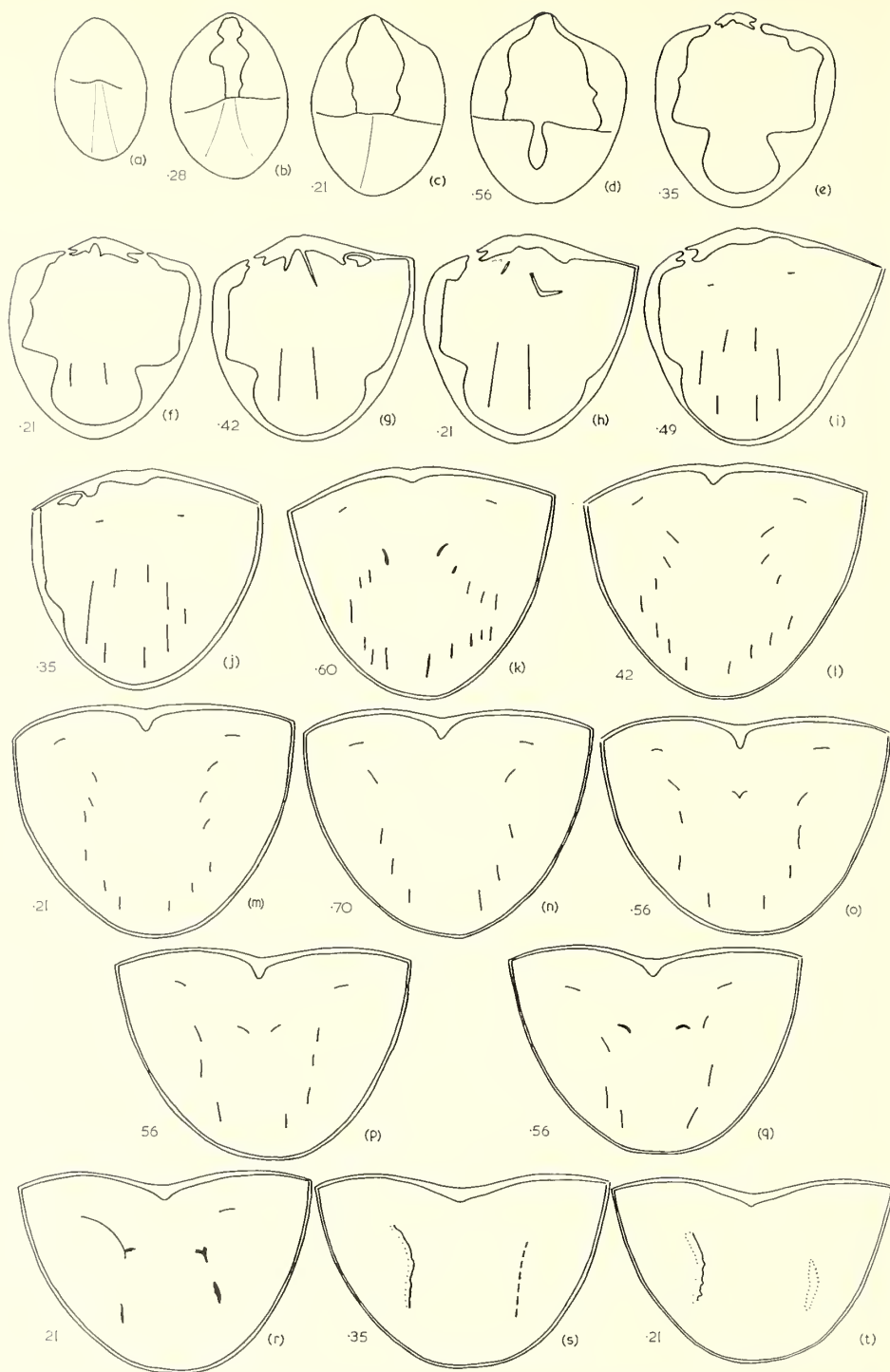
The crura arise from the inner margin of, and fuse with, geniculiiform inner shell surfaces which flank a septalium in the cardinal plate. Genuiculation commences on a level with the hinge axis and immediately adjacent to the shell mid-line. Its development is reflected in the micro-structure of the shell where a close relationship is seen to exist with the development of the septalium, beneath which concentration of growth-lines indicates a retarded rate of shell secretion (see Pl. 121, figs. 1, 2; text-fig 3).

The crura develop from the septalium walls as narrow rods and follow the line of the walls as they diverge at an angle of about 55° . Complete fusion and continuity of shell structure is rapidly achieved between each crus and the parent shoulder, which provides additional support.

The crura extend ventrally a distance equal to about one quarter the depth of the cavity, and curve gently with the convex edge facing anteriorly; they descend anterior to their point of origin. At their distal end they produce the primary lamellae which first extend laterally to a position near the dental sockets before descending anteriorly. Peels taken from the crura reveal lamellae of fibrous calcite parallel to the surfaces. There is complete continuity with the primary coil.

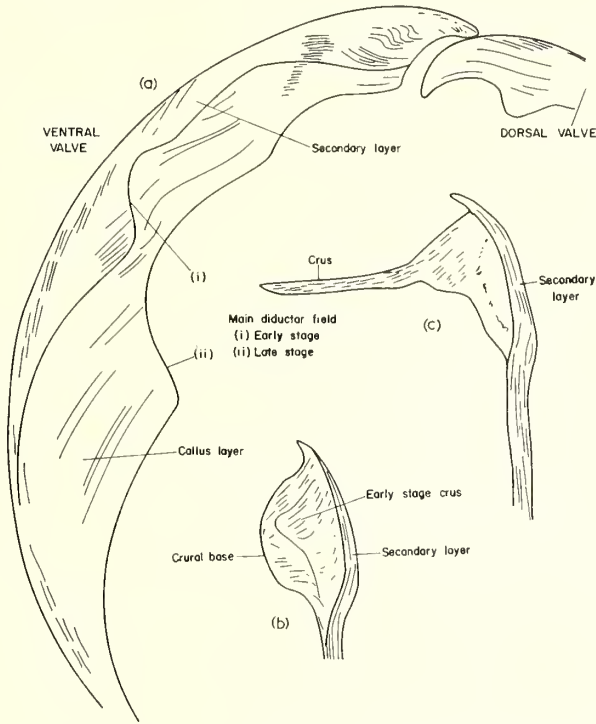
In longitudinal sections the micro-structure of the supporting crural base reveals a sharp projection within the secondary layer representing an early stage of crural development (see text-fig. 2). The base is supported on a flat spoon-shaped depression within the brachial shell.

The primary lamellae descend almost vertically at a position close to the outer socket ridge before producing the first coil. The first four or five coils are strongly flexed along their dorsal arc (text-fig. 1 and Pl. 119, fig. 10). Up to nine coils are contained in each spire, flexuring being less pronounced on each successive coil. The coils are more widely spaced dorsally than ventrally, hence the axis of rotation of successive coils migrates ventrally. Alexander (1947, p. 308) aptly describes each spire as being '... shaped like a sombrero with one half of the brim turned up'.



TEXT-FIG. 1. *Dayia navicula* (J. de C. Sowerby), Lower Leintwardine Beds, Downton Gorge, Herefordshire. Series of transverse sections drawn from cellulose acetate peels. $\times 5$.

The jugum, arising from a position low on the first coil, is V-form, the apex pointing postero-ventrally. It is sharply recurved at its union with the primary coils (text-figs. 1*p-r*). A jugal stem points posteriorly. There appears to be perfect continuity in the micro-structure of jugum and primary lamellae.



TEXT-FIG. 2. Features of shell micro-structure in *Dayia navicula* (J. de C. Sowerby). (a) longitudinal section through muscle platform of ventral valve to show the position of an earlier valve floor and muscle attachment region. (b) longitudinal section adjacent to crus showing crural base formed of callus and 'embryonic' crus. These are in turn supported by a spoon-shaped depression in the brachial valve. (c) longitudinal section through crus. All $\times 16$.

Fimbria extend from the anterior part of the primary coils and are directed anteriorly. They originate in pustule-like growths within the coils which produce surface corrugations when fimbria are not fully developed. The pustules generally point medially. Discrete pustules occur rarely on the lower part of the jugum.

Silicified specimens (Pl. 119, fig. 9) clearly show the fimbria; they attain a maximum length of over 0.175 mm.

Median septum. At its anterior end the median septum has the form of a low rounded ridge and is little more than an internal bulge complementary to the external sulcus in the brachial valve. In a posterior direction the septum is more prominent and ridge-like with broad, low, supporting buttresses on its flanks. Towards the hinge line secondary callus builds up over the median septum producing a more triangular form in

cross-section before the median septum fades into the lower part of the cardinal plate, the transverse profile becoming increasingly subdued.

Ontogenetic changes of the median septum are preserved in the micro-structure of the shell (text-fig. 3a, b). Within the secondary layer calcite was secreted about the mid-line, successive growth layers being inclined from the shell outer surface laterally inwards and gently convex outwards. The following stages can be recognized in the development of the median septum from this layer:

- (i) Simple fold of shell (see above);
- (ii) Addition of secondary callus producing buttresses which are to serve as supports to the median septum;
- (iii) Successive addition of calcite layers to produce the characteristic ridge form, there being little lateral addition of calcite at this stage;
- (iv) Concentration of growth lines over crest of median septum indicating suppression of development ventrally but the addition of calcite on the flanks producing a triangular form;
- (v) Extensions of process operating in (iv) to markedly increase the width; continuation of this process finally flattening out the floor of the brachial valve at the mid-line.

The full sequence is discernible within the brachial shell just below the hinge line. Peels show darker areas of more concentrated lamellae at intervals. They increase in number posteriorly and must represent growth pauses. One shell revealed at least five and possibly six such growth pauses.

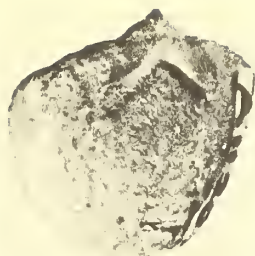
EXPLANATION OF PLATE 119

Figs. 1-7, 9-10. *Dayia navicula* (J. de C. Sowerby). 1, Upper Llanbadoc Beds, Darran, Usk, Monmouthshire. National Grid ST/327 979 (GSM 103292). Internal mould of ventral valve showing chevron diductor field, with the accessory diductor field in its apex, and the adductor muscle field. Between the adductor muscle impressions faint ridges (? vascula media) exist ($\times 7$). 2, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11207). Internal mould of ventral valve showing diductor muscle field in an immature specimen ($\times 5$). 3-4, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11202 and A11206). Internal moulds of brachial valve showing median septum, adductor muscle fields and position of dental sockets (both $\times 5$). 5, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11655-64 one of twelve specimens bearing number 2000). Lateral view of internal mould of ventral valve showing part of chevron and vascular markings (? gonadal sacs) ($\times 5$). 6, Lower Forest Beds, Llancayo, Usk, Monmouthshire. National Grid SO/372 036. Internal mould of ventral valve showing chevron diductor impression ($\times 6$). 7 and 11, *nilssoni-scanicus* zone, S. side of Mynydd-y-Gaer, Denbigh Moors, Denbighshire. National Grid SH/974 715. Internal moulds of ventral valves showing chevron diductor impression. Fig. 7 is an immature specimen also showing the adductor impressions ($\times 4$ and $\times 6$ respectively). 9-10, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11655-664 (specimen numbered 2042) and A11201). Silicified specimens showing form of spirillum. 9, lateral view exhibiting pustules and fimbria on spire, photographed through the silica mould (this specimen has been cut along the left side). 10, looking from the anterior ($\times 7$ and $\times 6$ respectively).

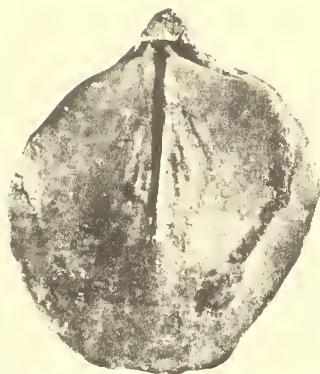
Fig. 8. *Dayia* sp. Köbbinghauser Beds (Lower Devonian), Huizinghausen, W. Germany. Internal mould of posterior part of ventral valve showing relatively small diductor muscle field ($\times 4$).



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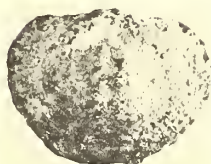
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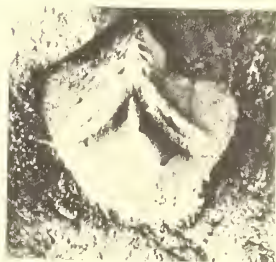
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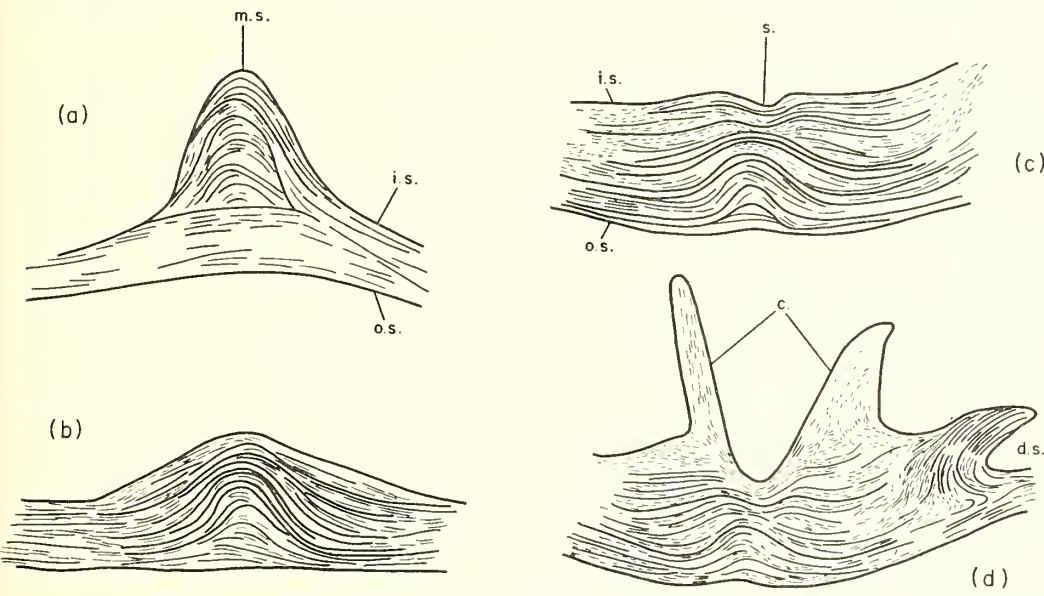
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11

Further changes can be recognized in the shell micro-structure at the mid-line but these are related to the changes in the cardinal plate.

Cardinal plate. Serial sections and latex casts provide no indication of the kidney-shaped cardinal process ascribed to *Dayia navicula* by Alexander (1947, p. 307). Instead, it is seen to have the form of a flattish or gently arched area lying within the brachial hinge plate, divided by a pronounced cleft or septalium. Suppression of the median septum by lateral addition of callus, as described above, reaches its ultimate conclusion in the



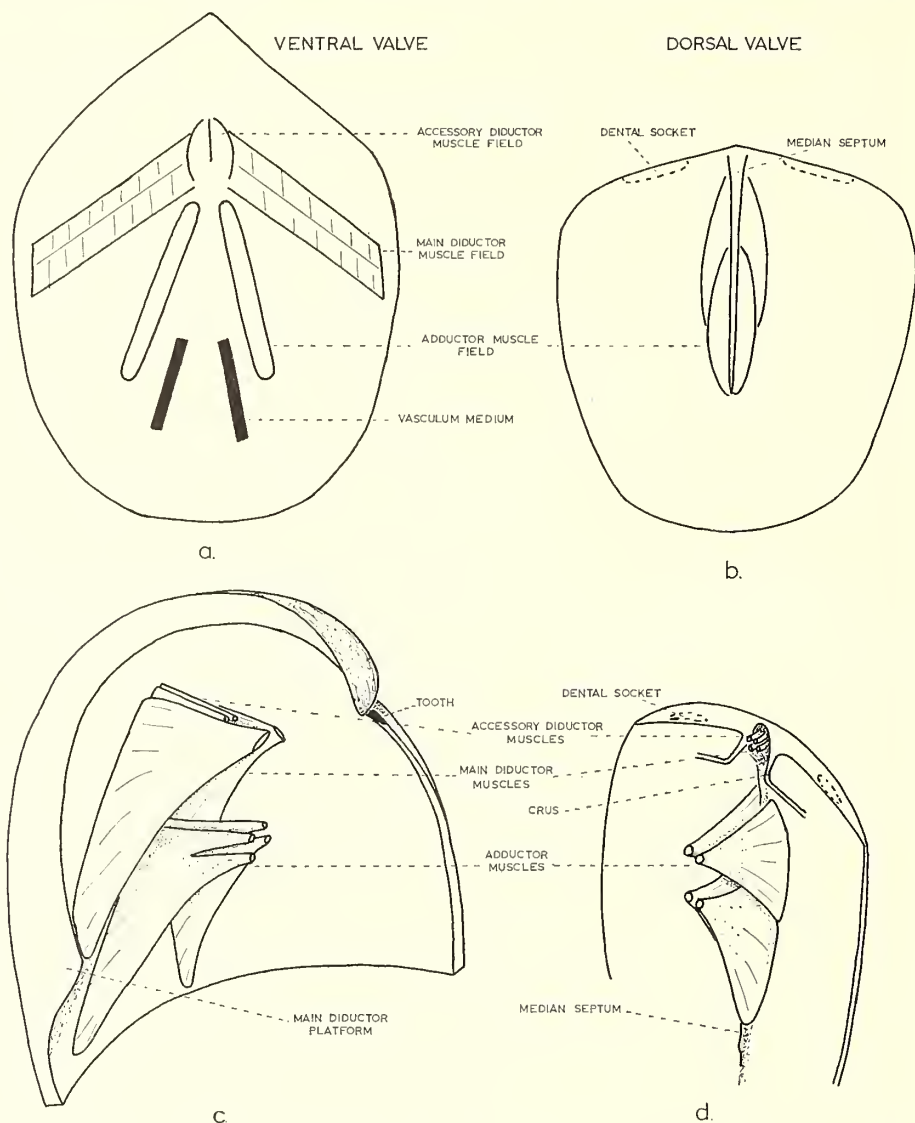
TEXT-FIG. 3. Micro-structure of shell of *Dayia navicula* (J. de C. Sowerby) at mid-line of dorsal valve (m.s., median septum; i.s., inner shell surface; o.s., outer shell surface; s., septalium; c., crura; d.s., dental socket). (a) transverse section through median septum $\times 45$ (b) transverse section through posterior part of median septum immediately below hinge line $\times 50$. (c) transverse section through cardinal plate below crura $\times 50$, and (d) including crura $\times 40$.

production of the cardinal plate. From then onwards crowding of growth-lines and growth pause at the centre-line reverses the form of the inner shell surface to produce the septalium (text-fig. 3 and Pl. 121, fig. 2). This trough is flanked by the crura and is in part a result of the development of the crura and expansion of the inner socket ridge.

Musculature. There is clear evidence for the former position of certain muscle fields but the interpretation of these fields and of the particular function of the muscles is less easy to deduce.

The pedicle valve contains a prominent chevron muscle-scar impressed on a platform produced by the addition of secondary callus to the inner shell surface. The muscle field occupies much of the shell width in mature specimens but only one-third of the width in juveniles (Pl. 119, figs. 1, 2). The apex of the chevron is directed posteriorly and extends to a point level with or even above the hinge-line; however the major part of the muscle field lies below this line. Two muscles occupied this field, one each side of

the shell mid-line, and they diverged at angles between 90° and 100° . One or more narrow troughs, or sometimes ridges, cross the field parallel to its long axis. Weaker, but more numerous, corrugations cross this line obliquely subparalleling the shell



TEXT-FIG. 4. Muscle fields and postulated form of muscles in *Dayia navicula* (J. de C. Sowerby).

mid-line. These are muscle tracks. The first set probably result from the anterior extension and migration of the muscle attachment areas during growth. This migration is demonstrated by the micro-structure of the supporting platform where the secondary addition of calcite is seen to obliterate earlier muscle fields which now lie ghost-like

within the layer of callus (see text-fig. 2). The oblique structures are believed to be due to the lateral extension of the muscle areas.

Situated in the apex of the chevron is a small elliptical area often divided by a trough (text-fig. 4 and Pl. 119, fig. 1). The limits of the area are strongly defined and the area must have provided an attachment region for separately functioning tissue—probably muscular.

Together, the above muscle fields are here interpreted as the diductor muscle attachment areas, the main diductors being attached to the chevron field and accessory diductors to the elliptical field. This interpretation differs from that placed upon the muscle-fields by Alexander (1947, p. 308, text-fig. 3).

Anterior of the diductor muscle platform in the ventral valve two slightly divergent troughs are weakly impressed into the shell: they are not always discernible. They extend from a position close to the lower apex of the diductor chevron halfway towards the anterior margin of the shell. The troughs exist in most growth stages but are most prominent in mature shells (Pl. 119, figs. 1, 7). These features were not recorded by Alexander; the present writer interprets them as the ventral muscle-fields of the adductor muscles.

In the umbonal region of the ventral valve other corrugations exist on the inner shell surface. Certain of these seem to have been interpreted as diductor muscle fields by Alexander but it is difficult to understand how the muscles could function mechanically if this interpretation is correct. These corrugations are possibly responses to folding of the mantle following pedicle atrophy. Alternatively they may represent pedicle attachment areas during early stages of growth, although their size tends to preclude such a simple interpretation.

No muscle scars are preserved on the cardinal plate. However, the adductor muscles left prominent impressions on the floor of the brachial valve. Although exhibiting some variation in form, these are normally elongate twin fields, the posterior field embracing half its companion (Pl. 119, figs. 3, 4). The muscle fields lie partly on the flanks of, and are separated by, the median septum which acts in part as a myophragm.

The writer's interpretation of the muscle fields is shown in text-fig. 4, together with a reconstruction of the form of the muscles as they crossed the visceral cavity. During youth the disposition of the (small) diductor muscle fields in the ventral valve and the cardinal plate in the dorsal valve permitted shell opening probably by uniform contraction of the muscles. In mature forms however the posterior arching of the ventral valve transposed part of the main diductor field to a position posterior of the hinge axis. It was inevitable therefore, that the main functional part of the muscle was that part lying below or anterior of the hinge axis and the main diductor muscles became extended anteriorly, with accompanying anterior extension of the muscle platform.

Vascular markings. Faint vascular markings are discernible between the diductor muscle field and hinge extremity in the ventral valve of mature individuals and also anterior of the muscle fields in both valves (see Pl. 119, figs. 1, 5). Saccate or lemniscate gonadal sacs can possibly be inferred from fig. 5 whilst fig. 1 shows divergent ridges between the ventral adductor scars which may indicate the former site of the vascula media. Other sinuses have not yet been recognized in *Dayia navicula*.

General micro-structure of the shell. Certain aspects of the micro-structure of the shell have already been discussed and many points of detail can be interpreted from text-figs. 2 and 3 and Plate 121.

The inner secondary layer of the shell, composed of fibrous calcite, is more prominent than the primary layer. The lamellae lie parallel or subparallel to adjacent shell surfaces, notably the inner surface. Considerable secondary callus has been added at the inner surface particularly around the median septum and on the ventral muscle platform. In the latter instance, as well as assisting change of muscle position it partly accounts for the highly arched and elevated form of the posterior region of the ventral valve. Within the umbo of the ventral valve growth layers are concentrated together as a result of growth pauses.

The very thin primary layer is frequently lost. Lamellae are closely spaced and seem to be sub-parallel to the outer shell surface, though sometimes lying obliquely to it. Alexander (1947, p. 309) suggested that the lamellae are ‘. . . directed forward and inward’.

In the umbonal region of the ventral valve the continuity of shell structure is interrupted by a number of ‘suture lines’, seen in transverse section as distinct seams (sometimes followed by cracks (text-fig. 1a-b)). They may be represented by inflections in the shell microstructure in longitudinal section (see text-fig. 2). The most prominent suture crosses the shell transversely and descends antero-ventrally through the secondary layer meeting the valve floor at the diductor attachment area. Two weaker sutures diverge ventrally from near the mid-line of the transverse suture; they appear to fuse anteriorly and rapidly fade away. These structures are difficult to interpret but bearing in mind the modifications affecting the muscle platform during ontogeny it is not unreasonable to suggest that they either had a similar supporting function or at least defined the limits of the muscles during some early stage of the individual’s development. In this respect it is worth noting that a somewhat similar structure, a transverse plate (shoe-lifter process), is exhibited by the Ordovician brachiopod *Aulidospira* (see Williams 1962, p. 253) another member of the Dayiacea.

ALLIED FORMS

Dayia is not uncommon in rocks of Eltonian (Lower Ludlow) age in many parts of Wales and the Welsh Borderland. The major difference between these forms and *Dayia*

EXPLANATION OF PLATE 120

Variants of *Dayia navicula* (J. de C. Sowerby).

Figs. 1-3. *Dayia navicula* cf. *bohémica* Bouček, upper part of Přidoli Beds ($e\beta_2$), Bohemia. Dorsal, anterior, and lateral views of three growth stages (all $\times 4$).

Fig. 4. *Dayia navicula* (J. de C. Sowerby); Hemse Group (Lower Ludlow) Lau, Gotland, Sweden. Dorsal, anterior, and lateral views of a mature specimen. ($\times 4$).

Fig. 5. *Dayia navicula* (J. de C. Sowerby); Skala Beds, Ruchotina, Podolia. Dorsal, anterior, and lateral views. Ventral umbo imperfect ($\times 4$).

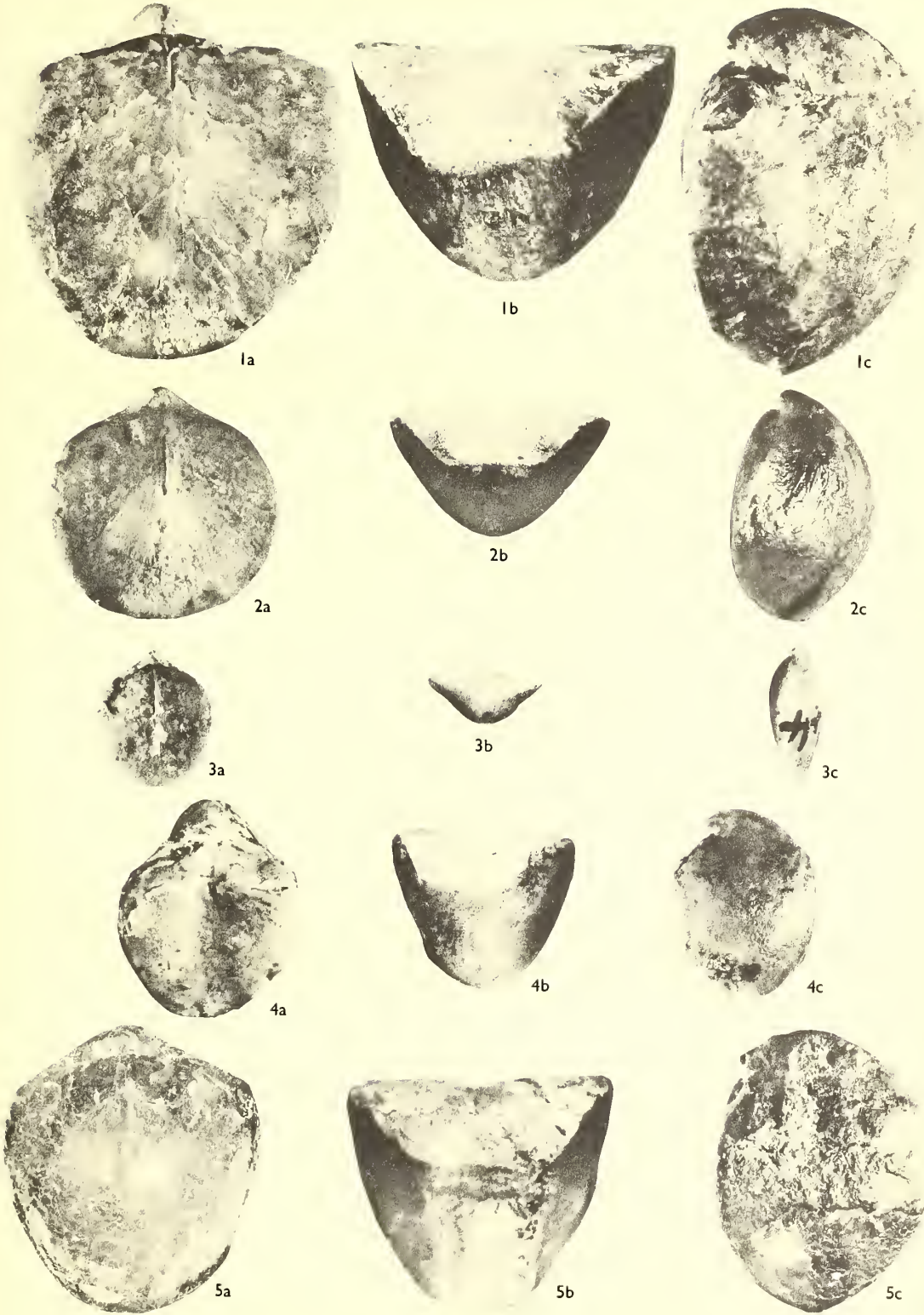
EXPLANATION OF PLATE 121

Microstructure of shell in *Dayia navicula* (J. de C. Sowerby). Photographs of cellulose acetate peels of calcareous shell, fig. 1 and 2 slightly retouched. All specimens from Lower Leintwardine Beds, Downton Gorge, Herefordshire. National Grid SO/431 733.

Fig. 1. Cardinal plate, showing shallow septalium (t.s. $\times 100$).

Fig. 2. Growth line pattern associated with socket, crus (proximal end) and septalium (t.s. $\times 125$).

Fig. 3. Pustules and fimbria on the lower part of the first coil of the spiralium (l.s. $\times 100$).



TUCKER, *Dayia*



1



2



3

navicula is their smaller size. Mature shells have an average length of between 7 and 8 mm. The degree of incurvature of the ventral umbo is similar although the posterior part of this valve is normally proportionately less elevated above the hinge line. Most specimens occur as internal moulds hence the external morphology is difficult to assess fully but there appear to be no fundamental differences from the typical form.

The internal structures are also the same although it has not been possible to interpret the spirallium fully. The intensity, but not always the length, of the chevron muscle scars and platform is similar, and the presence of additional impressions within the chevron supports the interpretation of the musculature. Specimens collected from the *Monograptus scanicus* zone of the Denbigh Moors (North Wales) show chevron muscle scars occupying at least two-thirds of the shell width (Pl. 119, fig. 11), a relationship which occurs in the Leintwardine Bed forms. Other specimens collected from the upper part of the Elton Beds (locally, Lower Forest Beds) near Usk possess proportionately smaller muscle fields which occupy approximately one-third of the shell width (Pl. 119, fig. 6). There is thus minor variation between the typical *Dayia navicula* and these earlier forms and also variation within the latter. It would however be premature to append varietal names until more comprehensive collections from rocks of Eltonian age are available for examination.

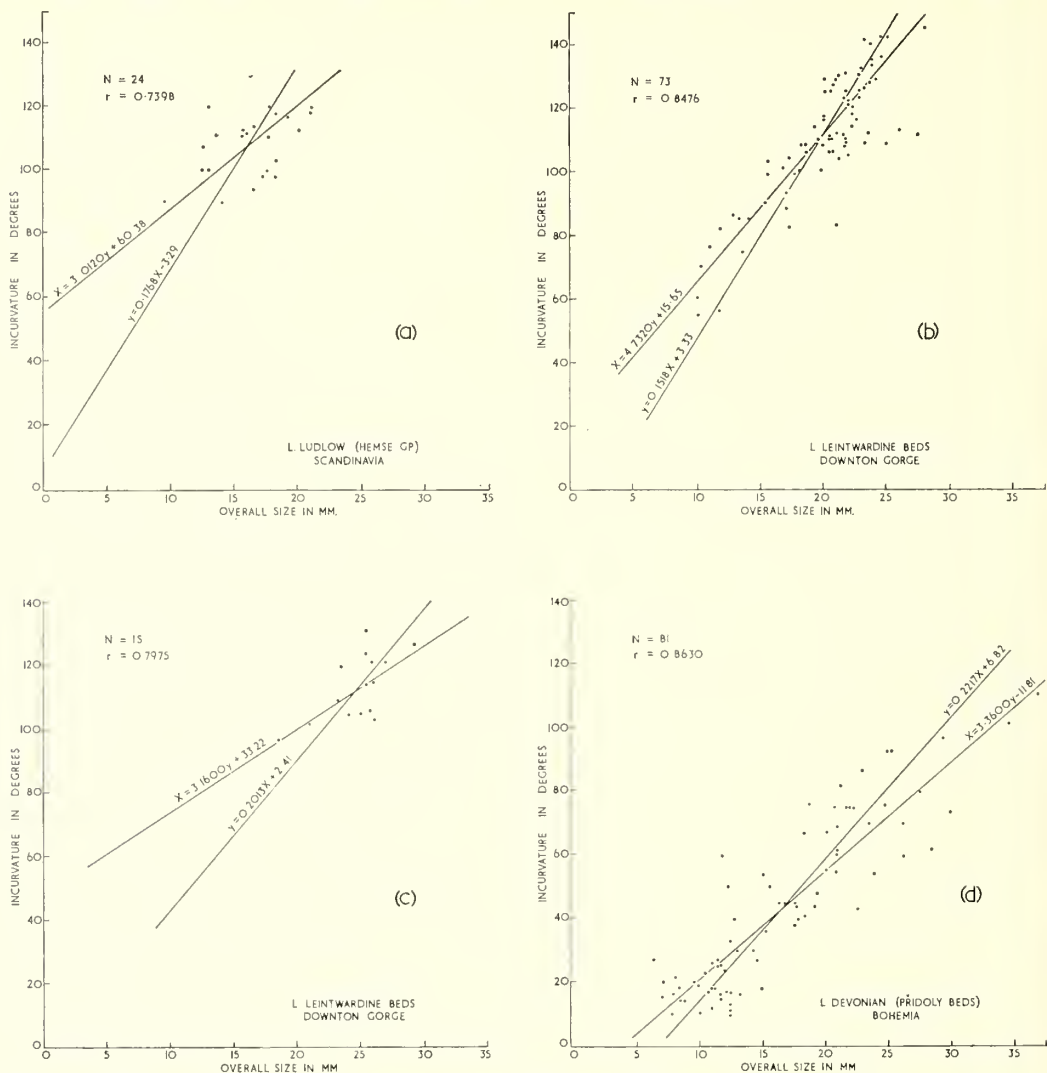
I am indebted to Dr. Anders Martinsson and Dr. H. Jaeger for providing me with specimens of *Dayia* from the Hemse Group (considered by Hede 1919 to belong to the zone of *Monograptus nilssoui*) of Scandinavia. No attempt at a full description is made here but the following points are worth noting. The average dimensions are similar to those of British Eltonian age but the posterior elevation of the ventral valve is greater than in the Usk form: the umbo is again strongly incurved (Pl. 120, fig. 4). The Scandinavian forms possibly possess closer relationships with the Denbigh Moor forms (which unfortunately have not yielded good externals although the moulds show a prominent umbonal feature). The chevron muscle field shows similar proportions to the Denbigh variety also. One characteristic feature of the Scandinavian forms is the almost horizontal disposition of the teeth; this is extremely rare in British forms. Almost all mature shells possess a deep sulcus and a strongly flexed lateral commissure.

Few Podolian specimens of *Dayia* are available for comparison. Kozłowski's description and illustration of this form in 1929, supplemented by material loaned to the writer by Dr. O. Nikiforova, show the close similarity between it and *Dayia navicula*. Minor differences in external morphology include a squarer outline to the brachial valve resulting from the straighter hinge and the fact that maximum width is attained closer to the hinge (Pl. 120, fig. 5). The shell is relatively less wide than British examples but with a deeper ventral valve, strongly incurved but less elevated at the umbo. The species occurs in the Marnes de Dźwinogród of the Skala Formation.

Similarities exist between certain Podolian and large Bohemian specimens (see below) but the Podolian specimens are closer to the British forms.

In 1940, Bouček discussed variation within *Dayia navicula* in Bohemia. He recognized two subspecies which he named *Dayia navicula minor* and *Dayia navicula bohemica*. They are recorded from zones $e\beta_1$ and $e\beta_2$ of the Budňany Beds which, according to Jaeger (1962 and 1965) range from the Ludlovian into younger beds. It is clear from Bouček's illustrations that the shape of both varieties is different from the typical British form. Horný (1955, p. 438) suggested that a transition exists between the two subspecies.

A collection of Bohemian *Dayia* from the Přidolí Beds (belonging to $e\beta_2$) have been studied by the writer. They include many growth stages. Based on external morphology



TEXT-FIG. 5. Scatter diagrams to show the relationship between incurvature of the ventral umbo and overall size (height + width + thickness) in four assemblages of *Dayia*. Assemblages *b* and *c* occur 22 and 55 ft. respectively above the base of the Lower Leintwardine Beds. *N*, no. of individuals in sample; *r*, degree of correlation between related regression lines.

alone, both Bouček's subspecies appear to be present. With the exception of one assemblage which may represent the true *minor*, mature individuals generally attain greater dimensions than the British form. The ventral umbo is less strongly incurved (see Pl. 120, figs. 1–3) and the foramen probably remained unimpaired until later in

life; hence pedicle atrophy was delayed. The diductor muscle platform is weakly developed. There is a suggestion of vestigial deltidial plates in some small juvenile shells, although the observed features could result from slight curvature of the ventral interarea at the delthyrium edge. Deltidial plates are not apparent in mature shells.

The hinge-line is straighter and proportionately longer than in British forms so producing distinctly squarish cardinal extremities. The shells are less elongate and the lateral margins are more sharply angular. Surface ornamentation is similar but the costae are more prominent.

The Köbbinghauser Beds of Germany and their age equivalent the Schistes de Liévin of Artois yield '*Dayia uavacula*'. This form is being studied by Dr. J. Shirley who in 1962 expressed the view '... that the "*D. navicula*" of these areas and Liévin differs specifically and constantly from the Middle Ludlow (i.e. *Leintwardine Beds*) form and is now to be referred to a new species *D. tenuisepta* sp. nov. (nomen nudum)'. A specimen from the Köbbinghauser Schichten is figured on Plate 119, fig. 8. It is larger than British forms but possesses relatively small and less prominent muscle attachment areas.

STRATIGRAPHICAL CONSIDERATIONS

The true nature of the sequence of faunas in the various Siluro/Devonian successions of Great Britain and Continental Europe is now more fully understood than a few decades ago and closer agreement is being reached on correlation. Following Jaeger (1962 and 1965) it is apparent that *Dayia*-bearing strata in the Rhineland, Artois, Bohemia, and Podolia are younger than the British Ludlovian. Jaeger shows that *Monograptus* extends upwards at least to the top of the Middle Siegenian in Germany and Bohemia. Teller (1964, table 5) for Poland, also shows graptolites in beds younger than the British Ludlow Bone Bed. Correlation between graptolitic and shelly facies in these areas and adjacent Podolia demonstrates the high stratigraphic level attained by *Dayia* and emphasizes the inapplicability of the genus as an index of Silurian rocks. The characteristic British forms and the, in part contemporary, Scandinavian forms are ancestral to these other varieties.

A study of assemblages separated in time brings out a fundamental change in external morphology during phylogeny. Text-fig. 5 shows the relationship between incurvature of the ventral umbo (see Tucker 1965, fig. 2) and overall size for four assemblages ranging in age from Lower Ludlow to Lower Devonian. Regression lines have been computed for each assemblage. The lower degree of correlation of samples (a) and (c) is due to the low number of individuals and lack of juvenile forms in both samples. However, it can be seen that during phylogeny individuals tended to attain greater dimensions whilst incurvature was progressively delayed and less intense. These changes are most pronounced in the assemblage of *Dayia navicula bohémica* from the Lower Devonian of Bohemia. The reduced rate of hooking would clearly postpone pedicle atrophy, a condition facilitating survival of the individual under a wider range of environment than the quiet water conditions suggested for *Dayia navicula sensu stricto* by Tucker (1965).

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Sedgwick Museum respectively. Mr. White drew the author's attention to the uncertain status of the assumed holotype. He is also grateful to those others mentioned in the text who supplied him with specimens from abroad. Dr. F. A. Middlemiss kindly read the manuscript.

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E. V. TUCKER
Geology Department
Queen Mary College
London, E.1

PLANICARDINIA, A NEW SEPTATE DALMANELLID BRACHIOPOD FROM THE LOWER DEVONIAN OF NEW SOUTH WALES

by N. M. SAVAGE

ABSTRACT. *Planicardinia* is described as a new genus of septate dalmanellid occurring in deposits of probable early Siegenian age in New South Wales. The new genus, known only by the type species *Planicardinia caroli* sp. nov., is placed in the Mystrophoridae together with the genera *Mystrophora*, *Kayserella*, and *Hypsomyonia*. It is the earliest known representative of the family and its presence at this horizon indicates that the origins of the group are at least as old as the early lower Devonian.

SEPTATE dalmanellid brachiopods have received considerable attention since 1953 when Havlíček described the new Middle Devonian genus *Prokopia*. In 1955 Cooper re-examined the Middle Devonian forms *Kayserella* and *Mystrophora* and proposed the new Middle and Upper Devonian genera *Phragmophora*, *Hypsomyonia*, and *Monelasmmina*. More recently Johnson (1966) described the new genus *Vallomyonia* from the Middle Devonian of Nevada and Johnson and Talent (1967a) described the new genus *Muriferella* from the late Lower Devonian of south-east Australia, Nevada, and Arctic Canada.

The new genus described herein is from the early Siegenian Mandagery Park Formation near Manildra, New South Wales, where it occurs infrequently in a large silicified brachiopod fauna (Savage 1967, 1968). It is the earliest known representative of the Mystrophoridae and is therefore of particular interest. Little is known of the phylogeny or origin of this family and the new genus does not directly throw new light on the problem of a possible precursor. However it does show that a highly specialized mystrophorid existed in the middle Lower Devonian and that the ancestral forms of the family can be expected in even older strata.

Attempts to classify septate dalmanellid genera have resulted in several different schemes which disagree markedly. Nevertheless most authors believe the group to be polyphyletic with septate dorsal valves evolving independently in more than a single lineage. Cooper (1955) referred *Mystrophora* and *Kayserella* to the Mystrophoridae, *Phragmophora* and *Hypsomyonia* to the Onniellidae, and *Monelasmmina* to the Schizophoriidae. Wright (in Moore 1965) proposed that *Kayserella*, *Prokopia*, *Monelasmmina*, and *Phragmophora* be grouped into a new family, the Kayserellidae, with *Hypsomyonia* the sole member of another new family, the Hypsomyoniidae, leaving *Mystrophora* the only remaining member of the Mystrophoridae. Johnson (1966) and Johnson and Talent (1967a) referred the new genera *Vallomyonia* and *Muriferella* to the Schizophoriidae. These latter authors discuss possible phylogenetic relationships in some detail (1967a, pp. 44–6) and it is clear that they envisage three distinct groups. The genera *Muriferella*, *Vallomyonia*, *Monelasmmina*, and *Hypsomyonia* are all placed in the subfamily Draboviinae together with *Salopina* which is suggested as a possible ancestor, *Prokopia* and *Phragmophora* are separated as a second lineage, and a third group consists of *Mystrophora*, *Kayserella*, and the new genus described herein (see Johnson and Talent 1967a, p. 46).

It seems very probable that *Planicardinia* is closely related to *Mystrophora* and to *Kayserella*. The three genera have a number of features in common, of which most notable is the possession of a cruralium in the dorsal valve. Cooper (1955, p. 47) does not appear to have been convinced that the small cruralium in *Kayserella* was the sole attachment surface for the dorsal adductor muscles. Furthermore, Wright (1965, in Moore, p. H338) refers to the cruralium as a septalium and suggests that the adductor muscles were attached to the valve floor. However, Biernat (1959, p. 38) has demonstrated that some Polish specimens of *Kayserella* possess a cruralium extending half the length of the dorsal valve (Biernat 1959, pl. iii, fig. 7) and it now seems probable that this structure was a functional muscle platform.

Hypsomyonia appears to be more closely related to *Mystrophora* than to *Muriferella* and *Monelasmia*. It has a large elevated cruralium which clearly functioned as a muscle attachment surface and a typical mystrophorid pentagonal outline with an emarginate anterior margin. *Hypsomyonia* has therefore been assigned herein to the *Mystrophoridae*.

It is probable that additional material will eventually be found which will indicate the true relationships of the various septate dalmanellids. Meanwhile any classification is likely to be only tentative. It appears to the author that the septate genera with a cruralium form a distinct phylogenetic group and the classification below differs from that of earlier authors in this respect.

SYSTEMATIC DESCRIPTION

Phylum BRACHIOPODA

Suborder DALMANELLOIDEA

Superfamily DALMANELLACEA Schuchert 1913

Family MYSTROPHORIDAE Schuchert and Cooper 1931

Revised diagnosis. Small, ventribiconvex, dorsally sulcate Dalmanellacea with a long apsacline or anacline ventral interarea and a shorter anacline or hypercline dorsal interarea. Both the delthyrium and notothyrium are open. The ornamentation is costellate to subfascicostellate. The dorsal interior has a high median septum supporting a large cruralium, a bilobed cardinal process, and ventrally or ventro-laterally elongate brachiophores. The ventral interior has a short, wide muscle field with the adductor scars not enclosed by the diductor scars.

Genera included:

- Mystrophora* Kayser, 1871
- Planicardinia* gen. nov.
- Kayserella* Hall and Clarke, 1892
- Hypsomyonia* Cooper, 1955

Genus PLANICARDINIA nov.

Type species. *Planicardinia carrolli* sp. nov.

Diagnosis. A plano-convex mystrophorid with an anacline ventral interarea and a hypercline dorsal interarea. Heavy triangular teeth are supported by strong dental

lamellae. The dorsal interior has a small bilobed cardinal process, ventrally elongate brachiophores and a vertical spoon-shaped cruralium supported on a variable median septum.

Discussion. Known only by the type species, *Planicardinia* most closely resembles the Western European Middle Devonian genus *Mystrophora*, particularly in the features of the dorsal interior. Comparison with the type species of *Mystrophora* (Cooper 1955, pl. 11, figs. 45–9) shows a marked similarity in the form of the ventrally elongate brachiophores with a crescentic cross-section and the high spoon-shaped cruralium. The ventral interior of *Planicardinia* also closely resembles that of *Mystrophora* with a similar short thickened muscle field. However, the shell shape of *Planicardinia* is distinctive with the anacline ventral interarea and hypercline dorsal interarea together forming a prominent part of the dorsal surface of the plano-convex shell. Another difference is in the orientation of the cruralium which in *Planicardinia* is inclined almost normal to the dorsal valve floor, a feature clearly related to the extreme curvature of the ventral umbo which necessitates adductor muscles positioned almost parallel to the commissural plane (text-fig. 1). The ventral ‘median septum’ in *Mystrophora*, described and figured by Cooper (1955, pl. 11, fig. 50), has been observed in only a single specimen where it showed as a narrow slit in the internal filling of a calcined specimen. This slit probably represents the position of the high dorsal septum extending to the floor of the ventral valve.

Hypsonomyonia is easily distinguished from *Planicardinia* for it possesses a much less curved ventral umbo and an interarea which is apsacline and not anacline. Internally the brachiophores are more laterally directed so that they almost parallel the hinge line and the cruralium is more gently inclined.

Kayserella is also very distinct from *Planicardinia* externally. Like *Hypsonomyonia* it has posteriorly directed interareas and a less rounded outline. Internally the dorsal median septum is longer and the cruralium is much smaller and less upright. In addition, the brachiophores are much shorter.

Planicardinia carroli sp. nov.

Plate 122

Material. The species occurs very infrequently and only 16 specimens have been recovered from several thousand shells dissolved from a silicified limestone horizon. Of these 2 are complete shells with the valves conjoined, 8 are ventral valves, and 6 are dorsal valves. The specimen numbers used are those of the Palaeontology Collection, Department of Geology and Geophysics, University of Sydney. Specimen SU 19540 is designated the holotype. Other illustrated specimens are paratypes.

Description. Exterior. The shell is subcircular to subpentagonal in outline with the greatest width at about midlength. The cardinal margins are very obtuse and the anterior margin is emarginate to slightly rounded. In lateral profile the shell is plano-convex (Pl. 122, fig. 25).

The ventral valve is strongly convex with the umbo swollen and prominent. The beak is erect or incurved and appears to be commonly resorbed by the pedicle (Pl. 122, fig. 15). A long concave interarea is anacline and has an apical angle of about 130°.

The delthyrium, which has a width of about one-quarter that of the hinge-line, includes an angle of about 35° .

The dorsal valve is transversely oval to pentagonal in outline and planar or weakly convex. In the mature dorsal valves there is a distinctive convexity at the valve margin (Pl. 122, fig. 10). The umbo is poorly differentiated and the small distinct beak is postero-dorsally directed (Pl. 122, fig. 25). A long, slightly concave, hypercline interarea makes a very obtuse angle with the valve surface. (Pl. 122, fig. 25). It has an apical angle of about 150° . The notothyrium is open and includes an angle of about 50° .

A low broad sulcus in the dorsal valve extends from the beak to the gently sulcate anterior commissure. No distinct fold is present in the ventral valve. The surface is costellate with about thirty-four costellae 2 mm. from the dorsal beak. The costellae increase chiefly by intercalation.

Interior of ventral valve. In the ventral interior a broad, deep delthyrial cavity is bounded by short vertical dental lamellae which diverge anteriorly at about 40° (Pl. 122, fig. 26). The anterior edges of the lamellae recede slightly and meet the strongly curved valve floor at about one-sixth the distance from the beak. Deep lateral umbonal cavities are present. The teeth are strong and pointed with a triangular profile (Pl. 122, fig. 15). A short sub-triangular muscle field is slightly elevated on the thickened floor of the delthyrial cavity but individual scars have not been observed (Pl. 122, figs. 14, 26).

Interior of dorsal valve. The dorsal interior has a small bilobed cardinal process set deeply in the apex of the notothyrium. The brachiophores are ventrally elongate and blade-like, diverging from the valve floor at about 50° and continuous with the margins of the notothyrium for part of their length (pl. 122, figs. 7, 10). They are crescentic in cross-section and bluntly pointed. The sockets are deeply excavated into the posterior of the brachiophore bases just ventral to the interarea margin (Pl. 122, figs. 10, 21).

EXPLANATION OF PLATE 122

Planicardinia carrolli sp. nov.

Figs. 1–5. Ventral, dorsal, anterior, posterior, and lateral views of complete specimen SU 22665. Note the dorsally directed interareas and the strongly convex ventral valve (fig. 5) ($\times 6.5$).

Figs. 6–11. Ventral, dorsal, postero-dorsal, antero-ventral, lateral, and postero-ventral views of the isolated mature dorsal valve SU 19541 showing the very high brachiophores (fig. 10), large spoon-shaped cruralium, and the small bilobed cardinal process (fig. 9) ($\times 6.5$).

Figs. 12–14. Antero-dorsal, ventral, and dorsal views of broken ventral valve SU 22666. Note the deep, lateral, umbonal cavities and the elevated muscle-field ($\times 6.5$).

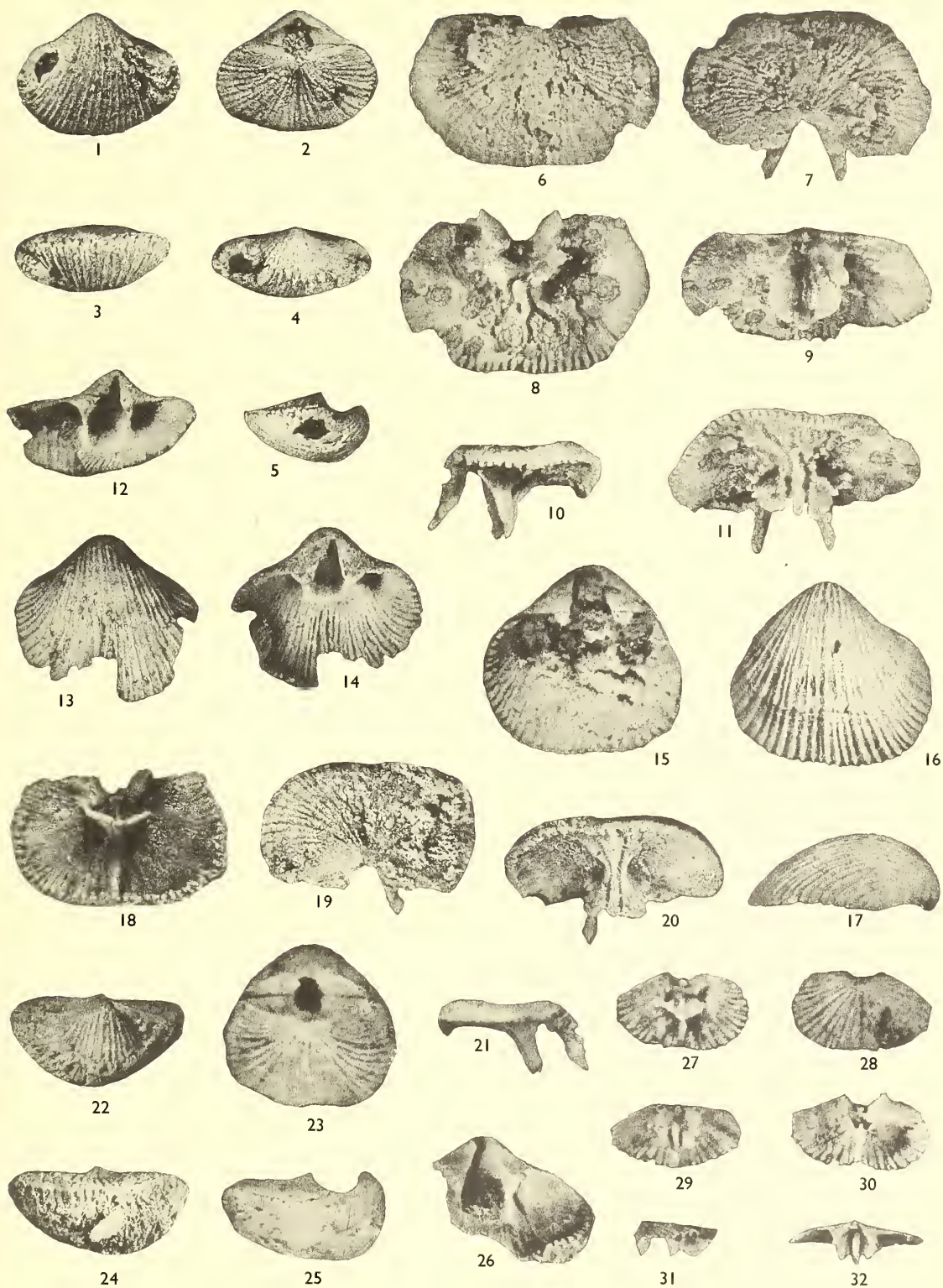
Figs. 15–17. Dorsal, ventral, and lateral views of ventral valve SU 19542 showing the resorbed beak, strong triangular teeth (fig. 15), and external ornament ($\times 6.5$).

Figs. 18–21. Ventral, dorsal, antero-ventral, and lateral views of mature dorsal valve SU 22667. Fig. 18 shows the spoon-shaped form of the cruralium and the degree to which the median septum has been almost totally resorbed ($\times 6.5$).

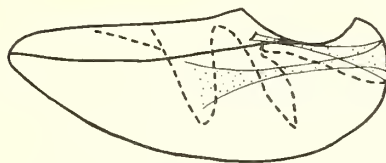
Figs. 22–5. Posterior, dorsal, anterior, and lateral views of complete specimen SU 19540 (holotype) showing the large dorsally directed interareas (fig. 23), the strongly convex ventral valve (fig. 25), and the gently sulcate anterior commissure ($\times 6.5$).

Fig. 26. Antero-dorsal view of broken ventral valve SU 19543. Note the strong dental lamellae and the thickened muscle area ($\times 6.5$).

Figs. 27–32. Ventral, dorsal, postero-ventral, antero-ventral, lateral, and posterior views of the young dorsal valve SU 19544 showing the relatively larger median septum extending into the cruralium (fig. 27), and sockets excavated into the bases of the brachiophores (fig. 29) ($\times 8$).



A high, almost vertical cruralium arises close to the brachioophore bases and extends anteriorly to about half the valve length. The spoon-shaped cruralium is supported by a high median septum which extends a little into the cruralium cavity and in young forms has a maximum elevation near the anterior valve margin (Pl. 122, figs. 18, 27, 31). The septum is much shorter in mature specimens (Pl. 122, figs. 8, 18). Adductor muscles were presumably attached to the inner surface of the cruralium but distinct scars have not been observed in the few specimens available.



TEXT-FIG. 1. *Planicardinia carrolli* gen. et sp. nov. Sketch to illustrate the position of the cruralium, brachioophores, and dental lamellae within a complete shell and the probable position of the adductor and diductor muscles.

The interior of both valves usually reflects the external costellation.

Measurements (in mm.)

		Length	Width	Thickness
SU 19540	Complete shell	4.2	4.3	2.1
SU 19541	Dorsal valve	3.6	6.1	—
SU 19542	Ventral valve	4.6	5.1 (est.)	—
SU 19544	Dorsal valve	1.5	2.6	—

Ontogeny. The very few specimens of this species include a young dorsal valve and two mature dorsal valves. In the mature specimens the median septum appears to be partly resorbed both anterior and posterior of the almost vertical cruralium, but in the young specimen it extends anteriorly almost to the valve margin and posteriorly well into the cruralium cavity (Pl. 122, figs. 27, 29). Another feature of the mature specimens is the extreme ventral elongation of the brachioophores and cruralium which greatly exceeds that in the small form (Pl. 122, figs. 10, 21). The large spoon-shaped cruralium seems to be deeply resorbed in one of the mature specimens by the two principal trunks of the lemniscate *vascula media* (Pl. 122, figs. 8, 11).

Occurrence. The species occurs in the silicified limestone horizon at the base of the Mandagery Park Formation 3 miles south of the town of Manildra, New South Wales, at Locality 1 of Savage (1968).

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N. M. SAVAGE
Department of Geology
University of Natal
Durban, Natal
S. Africa

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PROBABLE DISPERSED SPORES OF CRETACEOUS *EQUISETITES*

by D. J. BATTEN

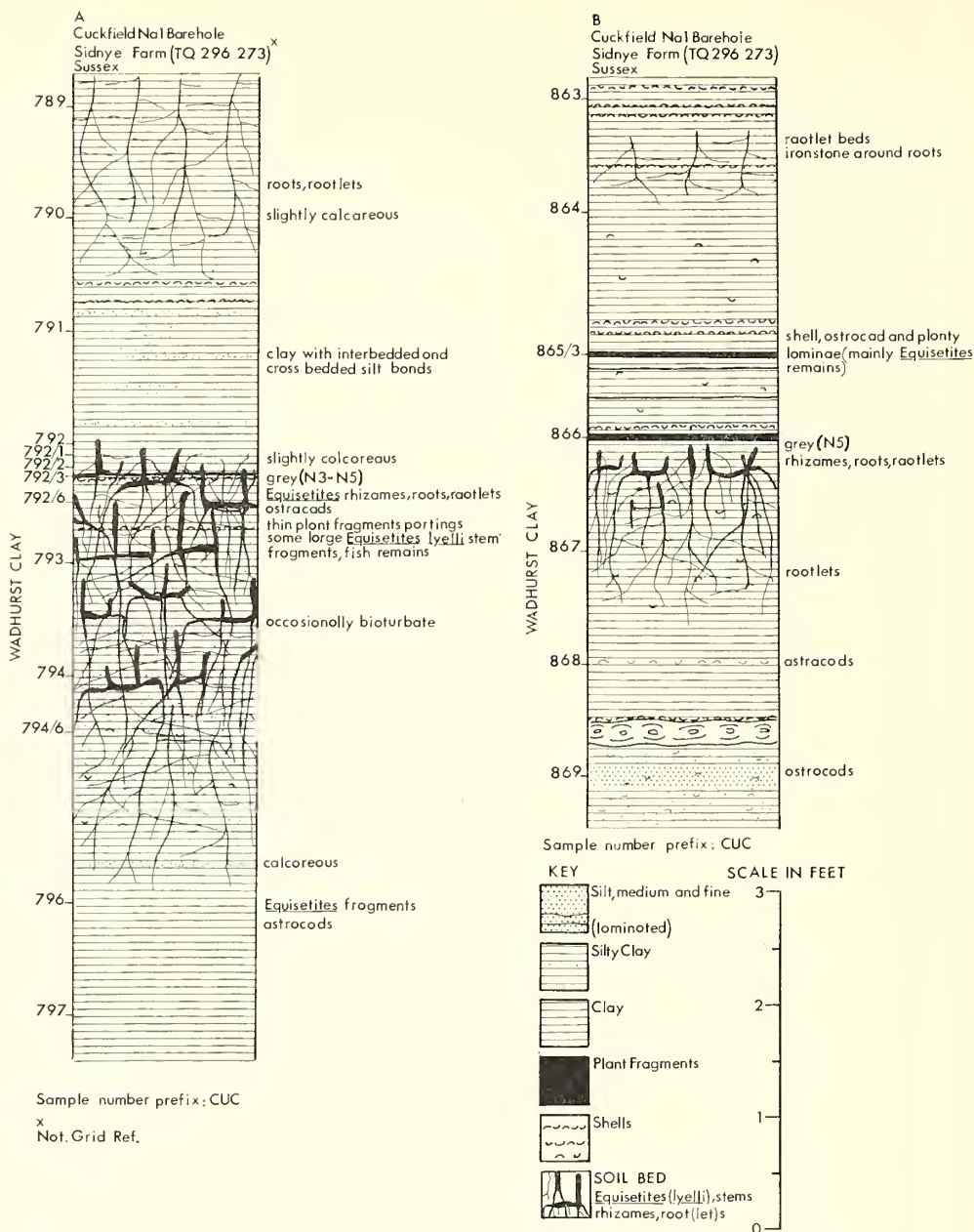
ABSTRACT. Dispersed spores that are considered to be those of Cretaceous *Equisetites* have been recovered from Wadhurst Clay (?Valanginian) sediments of southern England. They are described as *Pilasporites allenii* sp. nov.

IN the course of a study of the palynology of British Wealden delta sediments, the plant microfossil content of *Equisetites* soil-beds (in which rootlets, rhizomes, and stems of *Equisetites*, in various combinations, are preserved in situ) and partings with aerial debris of *Equisetites* (Allen 1941, 1947, 1959, 1967) was examined in the hope that the spores of these plants, which have not previously been recognized in Wealden sediments, might be recovered.

Samples used in this study came from Wadhurst Clay horizons in the Cuckfield No. 1 Borehole (Stubblefield 1967) and exposures at the Railway Brickyard, Sharpthorne, and in the lower clay pit at Freshfield Lane Brickworks, Danehill (text-figs. 1, 2). The soil-bed at Freshfield Lane Brickworks was recorded by Gallois (Stubblefield 1963, p. 37) as being 'the High Brooms *E. lyelli* soil-bed, some 25 ft. below the top of the Wadhurst Clay'. Fourteen soil-bed and fragment parting samples yielded a characteristic palynological assemblage dominated ($> 29.5\%$, based on a count of 200 specimens) by alete spores described herein from one of these assemblages as *Pilasporites allenii* sp. nov., and referred to elsewhere as cfA. *P. allenii* if not from the type assemblage, following the procedure recommended by Hughes and Moody-Stuart (1967b). Seventeen adjacent samples yielded assemblages in which these spores are frequent ($> 4.5- < 30\%$).

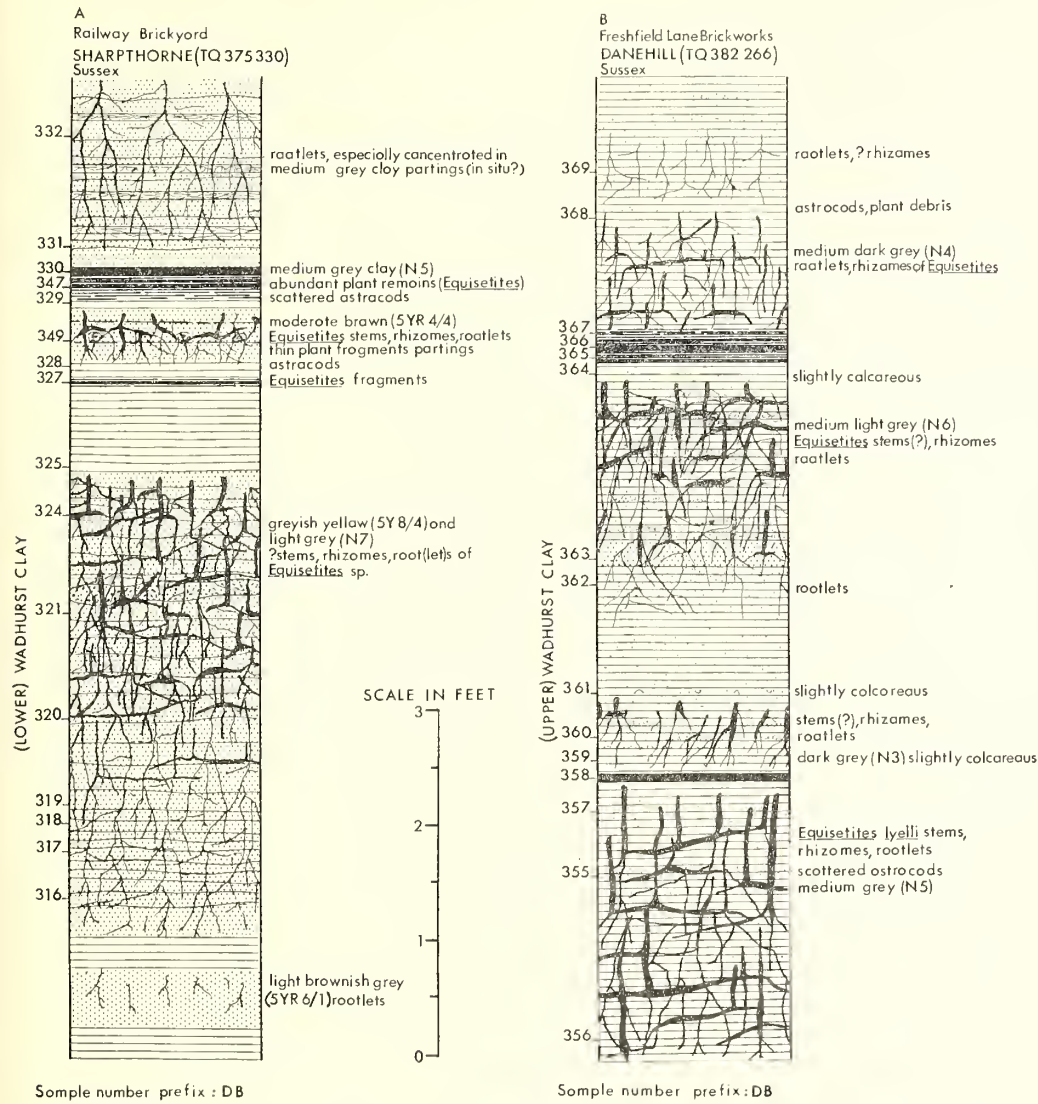
Although recently some authors have been using the names of living genera for Mesozoic plants, I consider that the convention of using a different name for Mesozoic plants is a useful one and should be retained. Thus, the name *Equisetites* has been used here rather than *Equisetum*.

The apparent absence from the palynological record of spores of *Equisetites*, the common Wealden macrofossil, has in the past been variously attributed to lack of preservation, recognition, or production. The restriction of assemblages in which the inaperturate spores mentioned above are dominant, to *Equisetites* soil-beds and fragment partings, is considered to be evidence in favour of an association of these spores with *Equisetites*. Of the 350 preparations I have made from Wealden samples, and of the many preparations in the Sedgwick Museum palynology collection, only those prepared from samples associated with soil-beds and fragment partings have yielded these spores in abundance. They have rarely been recorded from other palynological facies. The relationship was tested after the association had been recognized from the Cuckfield and Sharpthorne assemblages. I decided to prepare a further series of samples collected from Danehill where



TEXT-FIG. 1. A and B, Wadhurst Clay sediment cores from Cuckfield No. 1 Borehole. Details of lithologies (diagrammatic, obtained in part from the Geological Survey log) and horizons from which samples have been prepared for microscopical examination. The colour classification (see also text-fig. 2) is from the *Rock-Color Chart* (1963) published by the Geological Society of America. Colours have generally been noted when there is a departure from the predominantly grey (N3-N7) colours of the Wadhurst sediments. For the sedimentary rock nomenclature, a modified Wentworth grade scale has been followed. In beds where rhizomes and stems have not been seen but rootlets are recorded, it is likely that the latter are those of *Equisetites*. The medium grey clays (sometimes shales) are generally interlaminated with paler, generally very thin (< 1 mm.) siltstones. The presence of shells and ostracods has only been noted when they are abundant.

soil-beds and fragment partings had been observed in the field. The first samples processed were the fragment parting samples (DB 367, 366, 365, and 358) and I predicted that



TEXT-FIG. 2. A, Part of the (lower) Wadhurst Clay succession exposed at the Railway Brickyard, Sharpthorne, Sussex. B, (upper) The Wadhurst Clay succession exposed at Freshfield Lane Brickworks, Danehill. Details of lithologies (diagrammatic) and of horizons from which samples have been prepared for microscopical investigation. For 'Key' and other comments, see text-fig. 1.

they would yield assemblages in which cf *A. P. allenii* is dominant (> 29.5%). The prediction proved to be correct. Several of the soil-bed samples were subsequently found to contain an abundance of these spores (see Table 1 and text-fig. 2B).

A Cuckfield BH

SAMPLE No (prefix CUC)	789	790	791	791/11	792	792/1	792/2	792/3	792/6	793	794	794/6	796	797
cf <i>A. P. allenii</i>	0	8	3	31	58	25	22	60	5	X	3	X	11	X
Other inaperturates	7	14	10	10	X	10	12	8	11	11	7	12	13	10
bisaccates	54	32	34	13	9	27	20	5	28	26	29	21	30	43
<i>Classopollis</i>	4	8	X	2	X	2	2	X	3	2	4	X	5	2
total 'fern' spores	28	45	46	31	23	31	35	20	45	55	51	60	25	24
<i>Cicatricosisporites</i>	X	15	14	4	5	7	9	6	12	18	17	16	X	2

B Cuckfield BH

SAMPLE No (prefix CUC)	863	864	865/3	866	867	868	869
cf <i>A. P. allenii</i>	2	28	60	67	5	X	X
Other inaperturates	7	8	7	10	8	7	8
bisaccates	49	15	12	8	29	28	41
<i>Classopollis</i>	10	2	3	3	X	3	11
total 'fern' spores	23	38	14	9	54	54	25
<i>Cicatricosisporites</i>	2	4	2	X	8	11	5

C Sharpthorne

SAMPLE No (prefix DB)	332	331	330	347	329	349	328	327	325	324	321	320	319	318	317	316
cf <i>A. P. allenii</i>			56	54	9	6	5	30		X		X	2	2		
Other inaperturates	2	4	4	9	6	6	X	7	10	12	16	10	14	X	5	12
bisaccates	25	30	16	16	27	21	43	20	41	40	25	49	24	35	40	26
<i>Classopollis</i>	40	35	5	X	32	3	25	18	16	10	18	20	30	10	25	40
total 'fern' spores	26	22	11	16	19	40	18	22	12	25	31	18	16	16	25	14
<i>Cicatricosisporites</i>	10	6	X	4	X	15	2	X	X	X	2	X	X	X	X	X

D Danehill

SAMPLE No (prefix DB)	369	368	367	366	365	364	363	362	361	360	359	358	357	355	356
cf <i>A. P. allenii</i>	11	13	35	38	64	6	6	2	6	36	46	60	6	5	1
Other inaperturates	11	20	17	10	13	14	11	12	8	6	11	12	8	7	7
bisaccates	38	34	20	24	6	41	28	24	36	24	24	8	24	30	36
<i>Classopollis</i>	3	4	3	7	X	4	X	4		X			2	1	2
total 'fern' spores	33	25	19	18	8	26	49	49	39	28	14	16	54	54	48
<i>Cicatricosisporites</i>	5	4	3	X	X	8	10	11	8	8	2	X	10	12	10

TABLE 1. Distribution of cf*A. Pilasporites allenii* and major spore and pollen groups in some of the samples studied (see text-figs. 1 and 2) recorded as percentages, based on counts of 200 specimens. A and B, Cuckfield No. 1 Borehole. C, Railway Brickyard, Sharpthorne. D, Freshfield Lane Brickworks, Danehill. X indicates presence, but 1% or less. The absolute bisaccate and fern spore counts are fairly constant (see Hughes and Moody-Stuart 1967a) and are only apparently reduced in numbers when cf*A. P. allenii* or *Classopollis* are abundant due to their non-dispersal. The sample numbers are as they appear in text-figs. 1 and 2, from the highest point to the lowest point in the successions and not in numerical order.

DISCUSSION OF THE OBSERVATIONS

Although spores of *A. P. allenii* are usually frequent in the soil-beds, some horizons lack an abundance of these spores (Table 1). This may be for several reasons. The spore species in most of the soil-bed assemblages are poorly preserved. The poor preservation is partially related to sediment type which probably in turn partly reflects the environment of deposition. Allen (1947) stated that the Wealden *Equisetites* plants probably grew in shallow waters, colonizing a specific locality for a short period of time, perhaps for as little as three or four years. If, like living *Equisetum*, they grew predominantly in aerated waters, many of their spores may thus have been deposited in an environment, at times unfavourable for preservation, in which they were largely destroyed. When and where conditions were more favourable for preservation, indicated by the generally better state of preservation of most of the spore species, cf *A. P. allenii* is found preserved in abundance. Winnowing and subsequent dispersal of these spores in the waters of the Wealden basin could account for a lack of abundance in some horizons, and so could a low rate of spore production, or seasonal production and/or a rapid sediment accumulation rate in the soil-bed localities. Since the *Equisetites* communities were probably relatively local and only existed for short periods of time, even if the plants dispersed large quantities of spores frequently, the total number produced would be small when compared with the number produced by the plants living on the near-by land. Thus if *Equisetites* spores were dispersed over a large part of the Wealden basin, the chances of obtaining an assemblage in which they constitute more than 5% of the total number of spores counted is slight. If the plants did not produce large numbers of spores, as is possible, the likelihood is even less. They have not been observed to be more susceptible to corrosion than other dispersed spores, and in fact, when abundant, they are generally better preserved than the majority of bisaccates and some of the 'fern' spores in the assemblage. The poor preservation of the latter forms may however be due to reworking.

Some movement in the water (Allen 1941, p. 371), perhaps the result of storm wave action, at times caused the destruction of the aerial stems of the *Equisetites* plants and subsequent deposition of the fragment beds and partings. The fragments are preserved as flattened carbonaceous remains as opposed to stems preserved 'in situ' in which the pith cavities have generally been filled with sediment forming pith casts. The cones (strobili) of living species of *Equisetum* rapidly fragment after spore dispersal. If *Equisetites* cones similarly decomposed, it is unlikely that a mature cone would have been preserved in Wealden sediments. Only when a cone was prevented from reaching maturity, for example if the supporting stem was broken or the entire plant became suddenly inundated with sediments, would preservation be possible. Although a strobilus has yet to be recognized, cf *A. P. allenii* spore masses are frequently found, especially in assemblages extracted from fragment partings, and are probably microscopic remains of strobili (sporangia) broken up prior to or at the time of deposition.

Elaters which characterize the spores of living *Equisetum* have not been seen surrounding cf *A. P. allenii* or separated from them in any of the assemblages. They may have been destroyed during the preparation procedure. However, unless their chemical make-up is such that they are readily destroyed by the chemicals used during preparation, or were removed from the spores at the time of deposition and rarely fossilized, they should

be present in the palynological preparations. It is possible that the Wealden *Equisetites* species concerned produced spores which lacked elaters.

Apart from some Eocene *Equisetum* spores (Chandler 1964), and *Elaterites triferens* Wilson 1943, a Pennsylvanian tri-radiate spore, no other fossil spore species recorded to date possess elaters. They were not found surrounding the spores described from *Equisetites* compressions by Halle (1908), Hartung (1933), or Gould (1968).

Specimens recorded were all those present along selected traverses of strew slides. Stage co-ordinates refer to Leitz Laborlux (L1) microscope, number 557187, Department of Geology, Cambridge University. The slides have been deposited in the Sedgwick Museum palynology collection.

RECORD

Anteturma SPORITES H. Potonié 1893

Turma ALETES Ibrahim 1933

Subturma AZONALETES (Luber 1935) Potonié and Kremp 1954

Genus PILASPORITES Balme and Hennelly 1956

Type species. Pilasporites calculus Balme and Hennelly 1956, p. 64, pl. 3, figs. 60–4.

Remarks. Several genera have been erected for inaperturate miospores but their diagnoses are not distinct. I consider that it is not practical or helpful to attempt to distinguish this new spore from all published inaperturates of all ages; it is however, desirable and necessary to group it with and distinguish it from other Mesozoic inaperturates. *Pilasporites*, the late Palaeozoic (Permian) genus has therefore been selected instead of a Tertiary-based name. The alternative solution of erecting a new genus has been rejected because the primary purpose of this paper is to present an accurate account of the new species, rather than to classify it.

Pilasporites allenii sp. nov.

Plate 123, figs. 1–4, 6, 10–14

Type sample. CUC 792, Cuckfield No. 1 Borehole, Sidnye Farm, Surrey, England (TQ 296 273) from depth 792 ft. Wadhurst Clay, ?Valanginian. Medium dark grey (N4) clay, size of coarse fraction 25 μ ;

EXPLANATION OF PLATE 123

Figs. 1–4, 6, 10–14. *Pilasporites allenii* sp. nov.; spores from rock sample CUC 792, preparation T 210, $\times 1,000$. 1, Loose ?ektexine, dark area; T 210/10, L1 33.3 124.8. 2, Smooth form; T 210/1, L1 32.0 118.0. 3, Scabrate exine, development of major fold; T 210/5, L1 49.7 120.1. 4, Scabrate exine; T 210/1, L1 34.1 116.1. 6, More or less smooth exine, scabrate perine; T 210/1, L1 42.0 116.2. 10, Smooth exine, smooth crinkled perine; T 210/1, L1 34.7 117.1. 11, Smooth exine, closely adhering perine with granules and small verrucate elements attached to the perine; T 210/10, L1 29.0 123.4. 12, Dark area, scabrate, secondary folds developed around dark area; T 210/14, L1 55.0 126.8. 13, Split form; T 210/2, L1 30.8 123.3. 14, Split form; T 210/1 43.5 116.0.

Figs. 5, 7, 8, 9, 15, cf A. *Pilasporites allenii* sp. nov.; spores from rock sample CUC 792/3, preparation T 244, $\times 1,000$. 5, Showing dark area, only faintly visible; T 244/4, L1 27.7 118.1. 7, Major fold, loosened ?ektexine; T 244/4, L1 51.6 125.2. 8, Scabrate exine, major fold; T 244/4, L1 58.0 116.0. 9, Smooth exine, dark area, closely adhering smooth, crinkled perine; T 244/4, L1 28.1 116.0. 15, Scabrate exine, loose ?ektexine; T 244/4, L1 31.9 121.0.



BATTEN, Lower Cretaceous dispersed spores

thin fine silt laminations; *Equisetites* 'in situ' and fragments of the same. Preparation: oxidation 10 minutes Schulze solution, 3 minutes 5% ammonium hydroxide, mineral separation using zinc bromide; short centrifuging; strew slides, Clearcol and Euparal. Palynological facies: *Pilasporites allenii* well preserved, the bisaccates and some of the 'fern' spores less well preserved; 58% *P. allenii*, 23% total 'fern' spores of which 7% are *Ischyosporites* and 5% *Cicatricosisporites*, 9% bisaccates (based on a count of 200 specimens).

Diagnosis. Miospores, alete, mean diameter $36.7\ \mu$, standard deviation $5.36\ \mu$ (200 specimens), amb circular. Exine 1.25 – $1.75\ \mu$ thick, smooth, or scabrate. Frequently only one (major) fold present, usually developed close to and sub-parallel to the margin of the spore. Spores sometimes split (7% of the specimens), may be surrounded by a crinkled and folded perine *c.* $0.25\ \mu$ thick. Perine smooth or scabrate. An indistinct darker coloured area is seen on 4.5% of the specimens, averaging $14\ \mu$ in diameter.

Holotype. Slide preparation T 210/1, L1 42.0 116.2; Plate 123, fig. 6.

Description. Maximum diameter, observed limits 28 – $48\ \mu$; coefficient of variation 14.6%. 94.5% of specimens fall between 31 and $44\ \mu$ (text-fig. 3). Shape may be distorted by folding (Pl. 123, fig. 7), 2% of spores unfolded. Exine thickness not always readily measured owing to difficulty in obtaining an optical section. The outer layer of the exine (?ektexine) which carries the sculpture, may be loosened (brought about by oxidation) and simulate a closely adhering perine. No elaters seen. The darker area may result from a thickening of the exine. Usually these spores show folds developed only around and not across the area (Pl. 123, fig. 12).

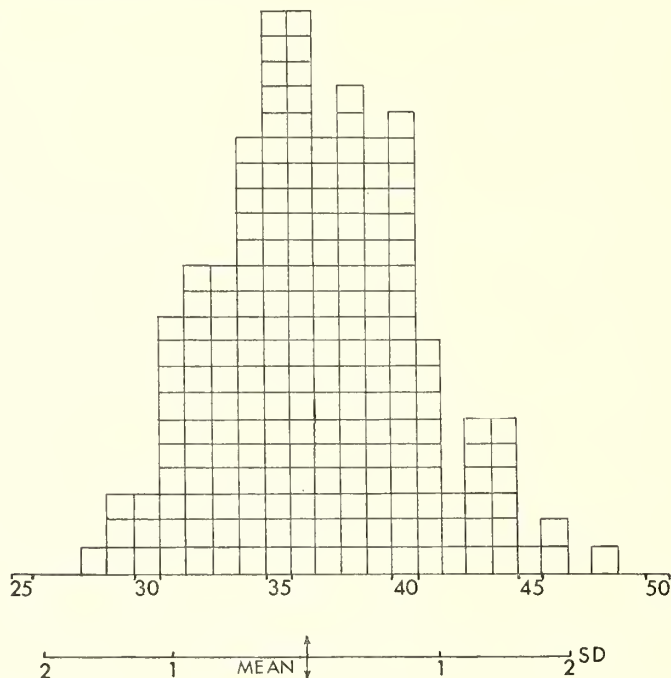
Preservation and compression. Preservation good. Spores occasionally unfolded but folds usually developed as mentioned above, probably resulting from the dehydration of the spore leading to the collapse of the spore wall in the subsequent compression. Spores very compressed.

Probable affinity. *Equisetites lyelli* (and ? other species of Cretaceous *Equisetites*).

Similarity of recent Equisetum spores. Observed acetolysed spores of 11 of some 25 living species of *Equisetum* (*E. hiemale*, *E. fluviatile*, *E. pratense*, *E. moorei*, *E. sylvaticum*, *E. arvense*, *E. telmateia*, *E. variegatum*, *E. scirpoides*, *E. palustre*, *E. ranosissimum*) lack a tri-radiate mark, and frequently lack elaters which separate from the spores during acetolysis. They are apparently smooth or scabrate spherical grains mainly 30 – $50\ \mu$ in diameter, surrounded by a sometimes scabrate folded perine. Specimens of some species show a tendency to split. Histograms of the diameters of spores of an individual species are unimodal, with a small standard deviation. Hauke (1963) states that in any one strobilus the size range of the spores is small, but strobili of different specimens of the same species may vary considerably perhaps representing differences in the age of the cones from which they come. Abortive spores also increase the size range obtained from an individual strobilus. Acetolysed specimens are frequently folded. Often only one major fold present (prep. TR002, *Equisetum telmateia*).

Distinction. Local: Couper (1958) erected the genus *Perinopollenites* for monoporate perinaceous grains, the presence of a pore being a diagnostic character although not

necessarily seen on all grains. The presence of the pore and a consistently firmly attached perine distinguishes this genus and its contained species from *Pilasporites allenii*. *Calamospora mesozoica* Couper 1958, a spore that is rarely definitely recognized in Mesozoic sediments, is distinct in possessing, by definition, a small tri-radiate mark similar to the dispersed spores of Palaeozoic *Calamospora*. *Spheripollenites scabratus* Couper 1958, differs from *P. allenii* in having a poorly defined pore, an internally scabrate exine, and in being smaller. *Exesipollenites tunulus* Balme 1957 possesses a circular depression surrounded by an area of exinal thickening.



TEXT-FIG. 3. Frequency distribution histogram of maximum diameters in microns of *Pilasporites allenii* sp. nov. Preparation T 210, 200 specimens, mean $36.7\ \mu$, standard deviation $5.36\ \mu$, coefficient of variation 14.6% .

Literature: Satisfactory comparisons are frequently difficult or impossible due to the inadequate descriptions and illustrations of the types. *Laevigatasporites maximus* Delcourt and Sprumont 1955, and the Tertiary species *L. intrapunctatus* Kedves 1961, differ from *P. allenii* in being much larger. *L. reissingeri*, a Tertiary species which Kedves (1961) refers to the 'Equisetaceae cf. *Equisetum*', is larger and has a thicker 'exospore'. *I. dubius* Pflug and Thomson 1953 has a thinner exine than *P. allenii*; *I. limbatus* Balme 1957, is larger, has a thinner exine, and possesses a dark peripheral band; *Araucariacites australis* Cookson 1947 is larger and has a different sculpture; *Pilasporites calculus* (Balme and Hennelly 1956, p. 64) has a differentially thickened exine; *Pilasporites plurigens* Balme and Hennelly 1956 is smaller; *Aulisporites* (Leschik) Klaus 1960, possesses an occasionally observable, faintly developed tri-radiate mark.

Comparison. Local: Similar spores from other samples or localities are attributed as suggested by Hughes and Moody-Stuart (1967*b*, p. 353).

cfA. *P. allenii* sp. nov.

1. Cuckfield No 1 Borehole, (TQ 296 273), depth 792 ft. 3 in., Wadhurst Clay, general size of coarse fraction of sediment 50 μ , *Equisetites* sp. soil-bed, *Equisetites* fragments; sample CUC 792/3, prep. T 244/4, preservation good, *Pilasporites* dominant. Maximum diameter 28 (35.5) 45 μ (200 specimens).

2. Cuckfield No 1 Borehole, depth 866 ft., Wadhurst Clay, general size of coarse fraction 8 μ , *Equisetites* sp. fragment parting; sample CUC 866, prep. T 269/2, preservation good, *Pilasporites* dominant. Maximum diameter 28 (36.8) 47 μ (50 specimens).

3. Sharpthorne, Sussex (TQ 375 330), (lower) Wadhurst Clay, general size of coarse fraction 50 μ , *Equisetites* sp. fragment parting; sample DB 330, prep. T 189/1, preservation moderately good, some pyrite and other corrosion, *Pilasporites* dominant. Maximum diameter 27 (35.8) 46 μ (75 specimens).

Literature: Reissinger (1950), Couper (1953), and Rogalska (1954) described and/or illustrated spores from Jurassic sediments which resemble *P. allenii*, and which they referred to the Equisetaceae (?*Equisetum*). *P. allenii* is also similar to *Pilasporites marcidus* Balme 1957, an Australian Cretaceous species, and to *Equisetosporites hallei*, the species that Nilsson (1958) erected for dispersed spores which he thought were similar if not identical to those produced by *Equisetites* (*Equisetostachys*) *suecicus* (Nath.) Halle 1908. Some of the specimens of supposed *Perinopollenites elatoides* grains which Danzé-Corsin and Laveine illustrate (in Briche *et al.* 1963, pl. 8, figs. 4–6) lack a pore and resemble *P. allenii*. Gould (1968) has described some remarkably similar spores from a cone of *Equisetum laterale* Phillips 1829 recovered from the Marburg Sandstone (Jurassic) of Australia.

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DAVID J. BATTEN
Department of Geology
Sedgwick Museum
Cambridge

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PALAEONTOLOGY

VOLUME 11 · PART 4

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THE STRUCTURE OF *VERTEBRARIA* *INDICA* ROYLE

by DIVYA DARSHAN PANT and R. SHANKER SINGH

ABSTRACT. Pulls of carbonised substance of Royle's type of *V. indica* and 250 other axes referable to the same species have been studied. The other specimens were collected from the Raniganj and Giridih coalfields (Permian; Upper Damuda Group, Gondwana System). They all show the same kinds of secondary xylem, large parenchyma, and phloem-like cells. The different kinds of pitting and their frequency in the tracheids, the frequency of uniseriate rays of different heights, their length, and the range of variation in xylem character, have been determined. It has been found that characters of xylem described for *V. raniganjensis* are within the range of *V. indica* and this species may be regarded as a synonym of *V. indica*. None of our several axes of *V. indica* shows any trace of pith.

ROYLE (1833) founded two species of *Vertebraria* from India (*V. indica* and *V. radiata*), that were later recognized as lateral and sectional views of the same fossil. By a strange coincidence McCoy (1847) and Dana (1849) made the same error in giving two names (*V. australis* and *Clasteria australis*) to laterally exposed and sectional views respectively of the same fossil. Arber (1905) and others have pointed out that all axes of this kind belong to a single species, *Vertebraria indica*, but Surange and Maheshwari (1962) have recognized two new species of the genus among compressions and Schopf (1965) has established a fourth species for a petrified axis, described earlier by Kräusel. However, a review of the literature on *Vertebraria* gave us the impression that the characters of the various species of the genus were neither sufficiently known nor clearly demarcated.

MATERIAL AND METHODS

A large number of specimens of *Vertebraria* were collected from localities in the coalfields of Raniganj and Giridih. About 300 celloidin pulls of coaly material were prepared from 250 compressions. The pulls were mounted in Canada balsam and examined in ordinary transmitted light under a compound microscope and also under phase contrast and dark field illumination. Averages have been generally calculated from 300 random counts but where this was not possible, the smaller number of counts has been mentioned against the averages.

All figured specimens and slides of this paper form part of Divya Darshan Pant Collection of plant fossils, located in the Botany Department of the Allahabad University.

DESCRIPTION OF EXTERNAL FEATURES

Compressions of *Vertebraria* axes are either found lying almost vertical to the bedding plane and seen in sectional views or they lie horizontally in the layers of the Lower Gondwana rocks and are exposed in a lateral view (Pl. 124, Pl. 125, figs. 1–2; text-fig. 1A–C). Sectional views of *Vertebraria* axes show rays of carbon, all joined and radiating from a centre and separated from each other by rather wide bays of rock matrix. The

rays are simple and almost equal, their ends may be slightly flattened, occasionally the surface of a bay may be covered by a film of carbon which joins two adjacent rays (Pl. 125, fig. 1). The largest vertically preserved *Vertebraria* in our collection is 2.7 cm. in diameter. Lateral views of horizontally compressed *Vertebraria* axes are more common. The thickest specimen in our collection is 9 cm. wide. The axes show 2 to 4 series of rectangular areas with 1 to 3 intervening longitudinal furrows or ridges. As a rule the rectangular areas are of almost equal size but sometimes they may appear very unequal (text-fig. 1B). Branching axes are not uncommon. As described by Oldham (1897) the branching of these axes takes place in two ways. Either the branching axis divides into two or more almost equal branches or the axes produce thinner branches from their sides (text-fig. 1A-C). The branches may show similar rectangular areas but some of the thinner axes have a central longitudinal groove or ridge and only occasional obscure horizontal marks (Pl. 124, fig. 5). Some of these axes show attached roots (Pl. 124, fig. 3). An attached root is also seen in a vertically compressed axis (Pl. 125, fig. 1).

As suggested by Pant (1956) the preservation of horizontally compressed *Vertebraria* is not fundamentally different from that of vertically compressed axes, except that their xylem rays radiating dorsally and ventrally become shorter or narrower in the radial direction by undergoing greater radial compression, while the radial dimension of their horizontally placed rays remains practically uncompressed. Naturally such axes are usually exposed along the plane of easier splitting, i.e., along the wider horizontally placed rays and these appear as two series of typical rectangular areas on either side of a median ridge or furrow representing the central longitudinal core of *Vertebraria* and the transverse sides of the rectangles represent the upper and lower limits of the wide parenchymatous bays. Occasionally the rock is fractured along one of the dorsally or ventrally placed vertically compressed rays (Pant 1956, text-fig. 2A, where towards the top left a few narrower rectangular areas are those of a vertically compressed ray). Additional longitudinal rows of rectangular areas may be seen at a point where a *Vertebraria* branches (text-fig. 1B; Pl. 124, fig. 2). Many of our axes lie among leaves of *Glossopteris*, *Rhabdotaenia*, *Pteronilssonina*, and other specimens. In one of these a *Glossopteris* leaf at first sight appeared to be connected with a *Vertebraria* but a closer examination reveals that the apical end of the leaf was actually facing the axis.

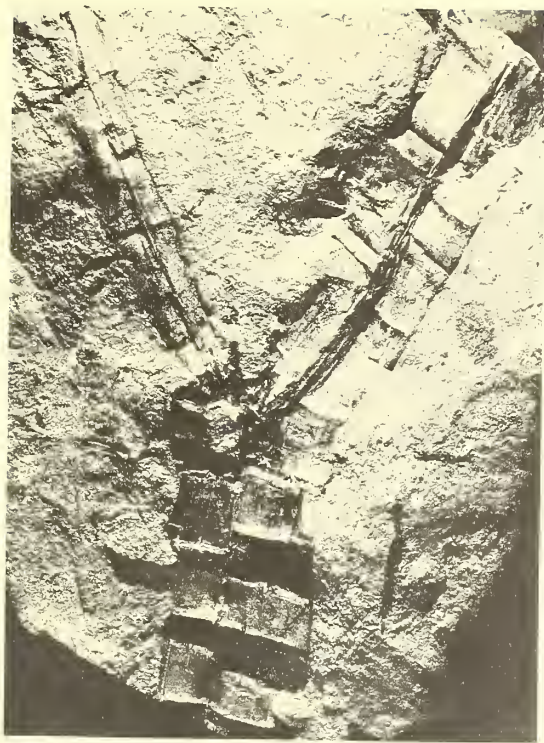
INTERNAL STRUCTURE

Horizontally compressed axes

Celloidin pulls of carbon from horizontally compressed axes and their branches with or without typical rectangular areas usually show the same kind of secondary xylem as

EXPLANATION OF PLATE 124

Figs. 1-5. *Vertebraria indica* Royle. 1, Forked axis, No. 1804, $\times \frac{6}{5}$. 2, Trifurcate axis showing wide rectangular areas in two series below and triseriate areas above; rectangular areas are not seen for some distance near the lower end; No. 1756, $\times \frac{2}{5}$. 3, Axis with elongated rectangular areas and a few thin branches (roots) with scalariform xylem (cf. *Lithorhiza tenuirama* Pant), No. 1805, $\times \frac{2}{5}$. 4, Fragment of a thick axis showing tetraseriate rectangular areas, No. 1808, $\times \frac{1}{2}$. 5, Axis with a median furrow but its rectangular areas are ill defined due to the presence of only a few rather obscure transverse marks, No. 3052, $\times \frac{4}{5}$.



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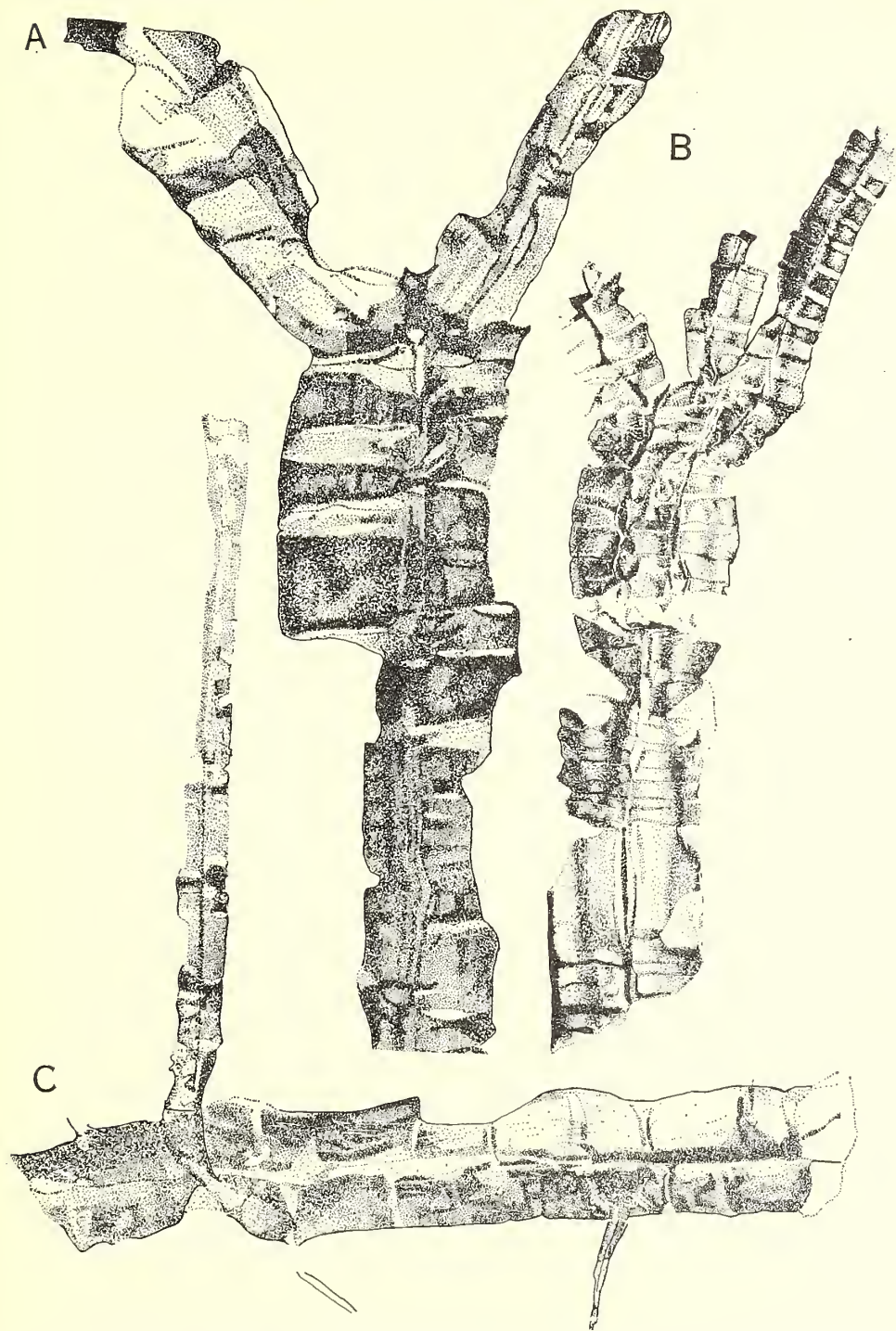
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TEXT-FIG. 1, A-C. *Vertebraria indica*. A, Axis forked into two almost equally thick branches, No. 1804, $\times 2$. B, Trifurcate axis showing short and wide rectangular areas above; rectangular areas not seen near the lower end (also Pl. 124, fig. 2), No. 1756, $\times \frac{1}{2}$. C, Axis showing thinner branch, No. 1789B, $\times 2$.

is seen in a radial section. Naturally, in compressed wood, such pulls also show the radial or tangential walls of the tracheids often overlapping each other. At a few places, the xylem is even seen in a tangential view or in a partially radial and partially tangential view (text-fig. 2H; Pl. 127, fig. 6).

Radial views of xylem. (a) Royle's type. A pull from Royle's type specimen No. V. 4189 in the British Museum (Natural History) shows the typical xylem of *Vertebraria* as if in a radial longitudinal section (Pl. 125, fig. 3). The tracheids have uniseriate to tri-seriate oval to circular pits placed far apart or contiguous. Biseriate and triseriate pits are usually opposite but alternately arranged pits have also been observed (text-fig. 3D, E). Rays are uniseriate and ray fields show pits usually without any border (text-fig. 3F). A few large parenchyma cells like those reported by Pant (1956) are mostly broken down.

(b) Specimens from Raniganj and Giridih coalfields. All our pulls of the carbon from horizontally preserved specimens of *Vertebraria* axes show well-preserved secondary xylem covering the entire surface of the rectangular areas (where carbon is preserved), from one side of the axis through the median ridge or furrow right up to the opposite side. On all our slides most of the xylem is seen as in a radial longitudinal section. A pith should have been visible in such radial views but no pull from the axes in our collection shows any trace of parenchyma cells in the centre, although ray parenchyma, phloem-like thin-walled cells and the typical large parenchyma cells of *Vertebraria* are usually well preserved. Instead, numerous pulls show undisturbed tracheids filling the central parts of the axes.

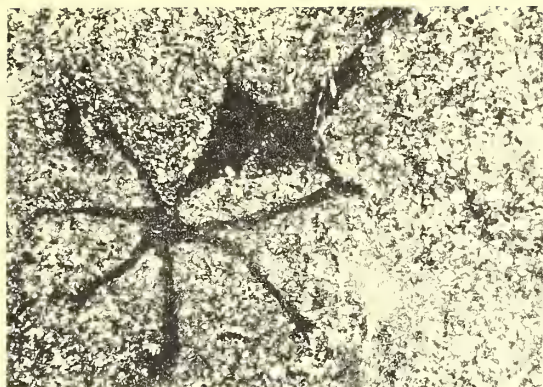
Primary xylem. Primary xylem tracheids consisting of scalariform, annular, or spiral elements were described from pulls of *Vertebraria* by Walton and Wilson (1932) and Pant (1956). Pant described them as occurring towards the periphery of the axes, where they could even have belonged to associated or attached roots.

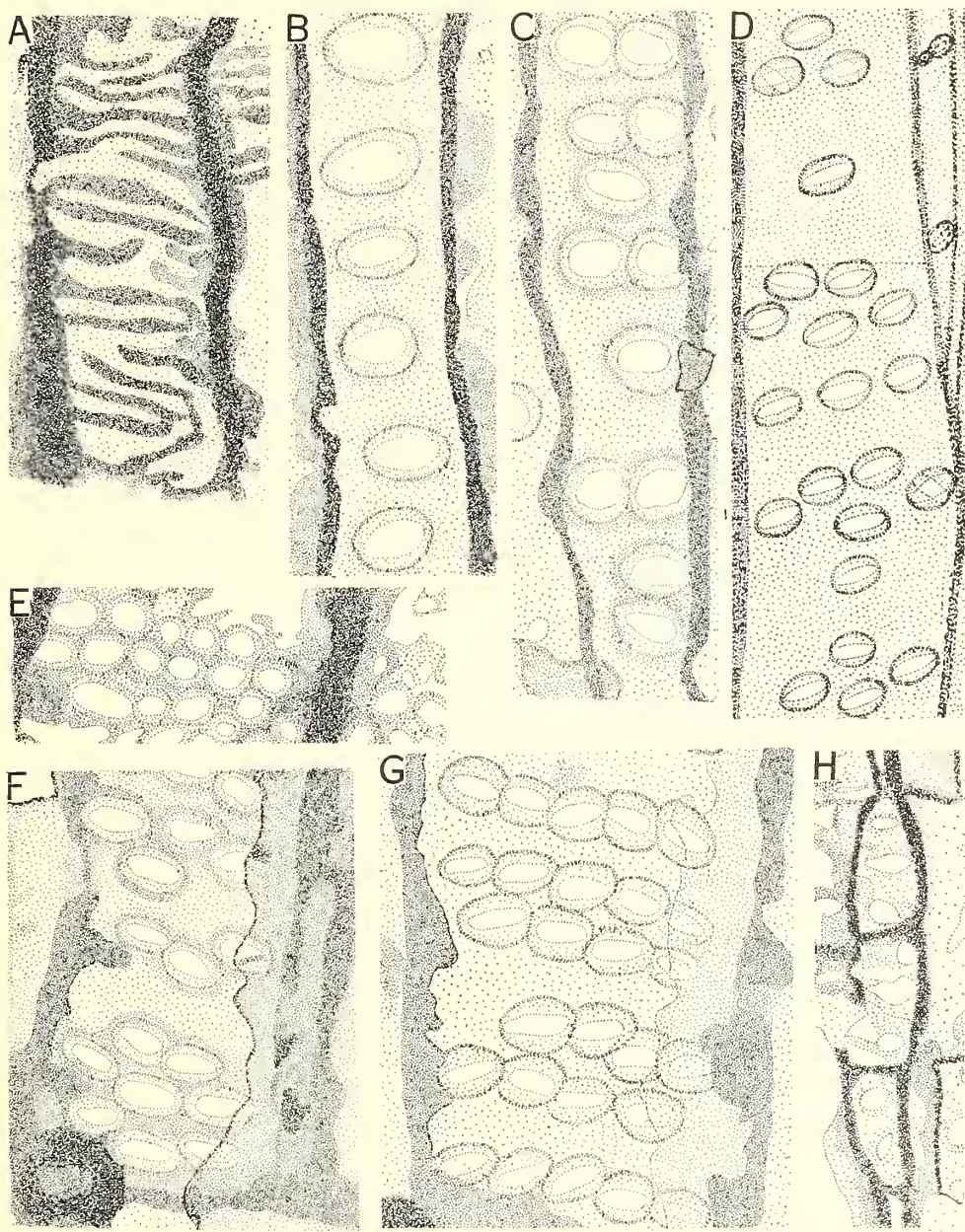
Secondary xylem. The wood is mostly secondary and pycnoxylic. The tracheids are almost all of a uniform type without growth rings. The length of most tracheids is indeterminable in the pulls and this may suggest that they were usually longer than the size of our pulls. However, 60 complete tracheids have been observed; their length is 77–679 μ (average 250 μ , δ 105). As both ends of most tracheids are not seen, we presume that these sizes may represent the shorter elements in the xylem of *Vertebraria*. The width of the tracheids ranges from 10–56 μ (average width of tracheids is 31 μ , δ 20.5). The tracheidal walls are up to 4 μ thick. The ends of the tracheids taper gradually to a narrow point, the end walls being very oblique (Pl. 126, fig. 1). The tracheids over the rectangular areas on the surface of the axes are straight and vertical but in the region of the horizontal ridges or furrows they are slightly curved.

Arrangement of pits. The pits on radial walls are uniseriate, or multiseriate up to 5 series of pits (text-fig. 2 B, C, and G). A single tracheid with 6 seriate pits was also seen (text-fig. 2 E, Pl. 126, fig. 2).

EXPLANATION OF PLATE 125

Figs. 1–6, *Vertebraria indica* Royle. 1, Vertically compressed axis towards the top right-hand corner; part of transverse diaphragm (black) and an attached root also seen; No. 1375, $\times 11$. 2, Vertically compressed axis showing marks of peripheral tissues, No. 1810, $\times 2$. 3, Pull from Royle's holotype showing biseriate and triseriate pits and a two-cell high ray, V. 4189, $\times 300$. 4, Xylem of root attached to axis in Plate 124, fig. 3, showing scalariform tracheids, Slide No. 1805, $\times 350$. 5, Portions of tracheidal walls of axis showing crossed pit pores, Slide No. 1809 Ba, $\times 500$. 6, Tracheids showing uniseriate pits or mixed uniseriate and biseriate opposite pits, Slide No. 1808c, $\times 800$.





TEXT-FIG. 2, A-H. *Vertebraria indica*. A, Portion of tracheid showing scalariform pitting (also Pl. 127, fig. 4); Slide No. 586, $\times 1,000$. B, Part of tracheid with uniseriate non-contiguous pits; Slide No. 1784 Da, $\times 750$. C, Portion of tracheid showing uniseriate and biseriate pits; Slide No. 1784 Da, $\times 750$. D, Irregularly-pitted tracheid showing oval pit-pores, some with crossed pit-pores; Slide No. 1807A, $\times 1,000$. E, Portion of wide tracheid showing 6-seriate pits (also Pl. 126, fig. 2); Slide No. 1807A, $\times 750$. F, Portion of tracheid showing oval groups of pits with a central pit; Slide No. 1765 C2, $\times 750$. G, Tracheid showing tetraseriate and pentaseriate pits; Slide No. 1767c, $\times 750$. H, Uniseriate 3-cell-high ray in tangential view; Slide No. 1784 Da, $\times 450$.

The pits may be contiguous or far apart (text-fig. 2 B; Pl. 125, fig. 5) and the portions of the same radial wall may be pitted in some regions and unpitted for varying distances in other regions. Multiseriate pits may be opposite, araucarioid (i.e. with crowded alternate pits having hexagonal outlines) or irregularly arranged (Pl. 126, fig. 3). As a rule unpitted portions of the wall are seen in tracheids with irregular pits. Some of these may show circular or oval groups of 3 to 9 pits (text-fig. 2 D, F). The same tracheid may show different kinds of pitting in different regions i.e., uniseriate or multiseriate, opposite or alternate, contiguous or non-contiguous (text-fig. 2 C; Pl. 125, fig. 6; Pl. 126, fig. 3). A random count of 300 tracheids showed about 11% with uniseriate pits, 47% opposite multiseriate pits, 12% alternate crowded multiseriate pits of araucarioid type, 28% irregular pits, and 2% showed portions of walls without pits. Out of the 47% tracheids with opposite pits 19% are biseriate, 18% triseriate, 8% tetraseriate, and 2% pentaseriate.

Shape and size of pits. The typical shape of bordered pits may be circular or oval (text-fig. 2 B). Oval pits in multiseriate tracheids are placed horizontally but where uniseriate they may be horizontal or oblique. The pit pores are generally oval but occasionally rounded. The two opposite pores of a pit pair are usually crossed (text-fig. 2D; Pl. 125, fig. 5). In the tracheids of the thinner axes pit pores are wide with a very thin border.

In some regions of the pulls, the tracheids show large horizontally extended oval pits where a border is not discernible. Such pits may be uniseriate or multiseriate. Where uniseriate they almost look like scalariform thickenings (text-fig. 2A; Plate 125, fig. 4; Plate 127, fig. 4) and where multiseriate they often appear transitional between typical scalariform and pitted elements. Pant (1956) described such tracheids as in contact with large parenchyma cells.

The circular pits are 4–8.5 μ (average 5 μ , δ 0.5). The length of the oval pits is 8.5–26.5 μ (average length is 13 μ , δ 2.5) and the breadth is 4–10 μ (average breadth is 6 μ , δ 1). The length of the oval pits whose borders are not clear is 10–31 μ (average length is 21.5 μ , δ 1.5) and the breadth is 4–10 μ (average breadth is 7 μ , δ 1).

Secondary xylem rays. Only uniseriate secondary xylem rays have been observed. These are 1–13 cells high (Pl. 126, fig. 5; Pl. 127, fig. 1), but more commonly they are only 1–4 cells high:

Percentage of uniseriate rays of differing heights

Height of rays in number of cells	1	2	3	4	5	6	7	13
Percentage	33	29	17	10	6	2	2	1

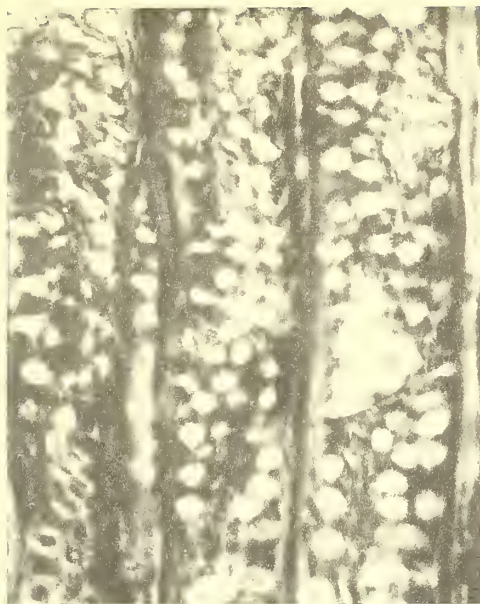
Frequency of rays per 10 mm.² is 4–18 averaging 9 (60 readings, δ 4). The rays are 1–48 cells long (average 11 cells, δ 4).

Crossfield pits. Crossfields of *V. indica* where clearly visible show 1–3 elongated oval pits (text-fig. 3A; Pl. 127, fig. 2). The oval pits are horizontally placed and seemingly simple. On the basis of our observations, we believe that the numerous bordered crossfield pits described by Walton and Wilson (1932) and by Surange and Maheshwari (1962) are pits of tracheidal wall, other than the common wall between a ray cell and a tracheid. In a compression, this wall may overlap a crossfield and then the pits can be mistaken for crossfield pits. The length of the crossfield pits ranges from 11–32 μ (average 18 μ , δ 2) and breadth from 4 to 14 μ (average 5 μ , δ 1).

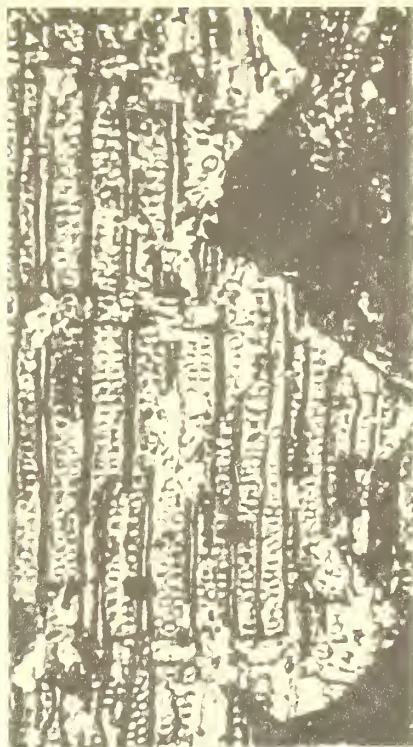
Phloem like cells. Many pulls show thin elongated cells by the side of xylem which look like phloem (text-fig. 3 C; Pl. 127, fig. 3). The length of these cells is from 17 to 238 μ (average 61 μ , δ 17) and breadth 4–35 μ (average 10 μ , δ 3). The thickness of the walls of these cells is up to 3 μ .

EXPLANATION OF PLATE 126

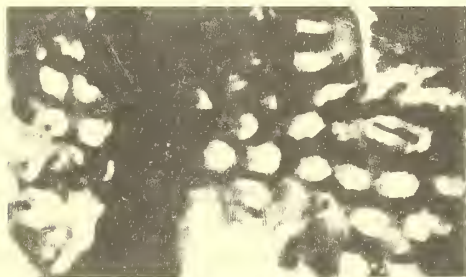
Figs. 1–5. *Vertebraria indica* Royle. 1, Xylem showing tapering ends of two tracheids and longitudinal walls of others with multiseriate pits, Slide No. 1807A, $\times$ 800. 2, Portion of wide tracheid (on the right side) showing six-seriate pits, Slide No. 1807A, $\times$ 800. 3, Xylem showing triseriate pits, opposite in some regions but alternate and araucarioid in other parts, Slide No. 1754C, $\times$ 350. 4, Pull from thinner axis with obscure rectangular areas showing typical *Vertebraria* type of xylem, Slide No. 1784 Db, $\times$ 140. 5, Xylem showing a 7-cell-high ray, Slide No. 1807A, $\times$ 200.



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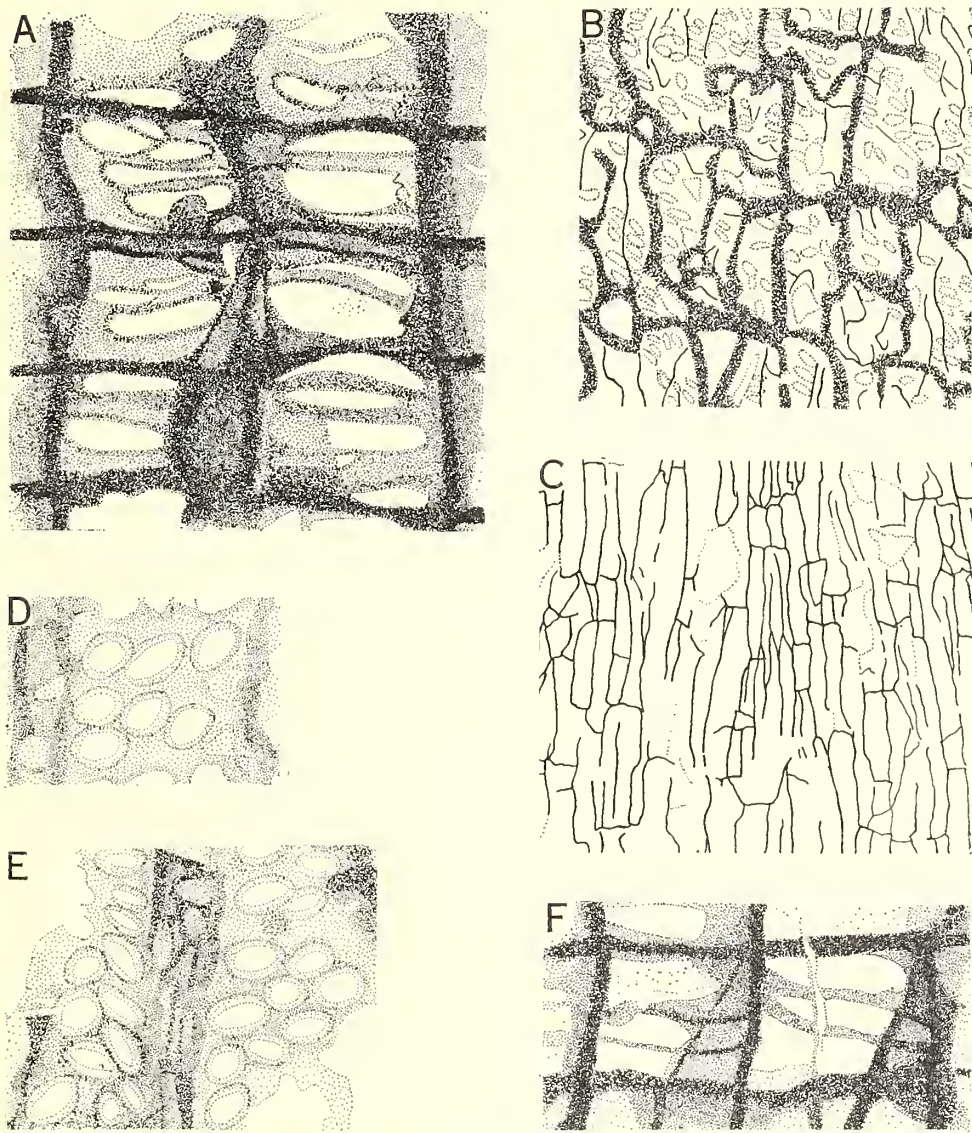
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TEXT-FIG. 3, A-F. *Vertebraria indica*. A, Portion of xylem showing simple, horizontally elongated, oval pits in cross-fields; Slide No. 1809 Ba, $\times 600$. B, Pull showing xylem with simple pits overlapped by broad parenchyma cells, which tend to be in radial series; Slide No. 586, $\times 150$. C, Pull showing thin-walled phloem like cells; Slide No. 1767A, $\times 150$. D, Portion of tracheid from holotype showing triseriate opposite pits; V. 4189, $\times 750$. E, Pull from holotype showing tracheid with uniseriate, biseriate, and irregularly arranged pits; V. 4189, $\times 750$. F, Xylem showing horizontally elongated, simple oval pits in crossfield; Holotype, V. 4189, $\times 750$.

Large parenchyma cells. In addition, sheets of large rectangular to polygonal parenchyma cells were seen overlying xylem almost in all preparations. Very often the cells tend to arrange in radial rows (text-fig. 3 B; Pl. 127, fig. 5). The length of these cells is 21–228 μ (average 79 μ , δ 49) and breadth 21–84 μ (average 34 μ , δ 17).

Tangential views of xylem. In portions of the pulls where the xylem appears in a partially or wholly tangential view, the xylem rays are seen and they are invariably uniseriate (text-fig. 2H). Where the rays are obliquely compressed, presenting a combination of tangential and radial views, the ray field pits appear to be simple and horizontally oval. The tangential walls of the tracheids are devoid of pits and their surface presents a uniformly granular texture (Pl. 127, fig. 6). The xylem of axes with obscure areas is essentially similar, showing identical pitting, uniseriate rays, crossfield pits, phloem-like cells and large parenchyma cells.

Vertically preserved axes

Xylem and other cells from vertically preserved axes are also indistinguishable from those of horizontally compressed *Vertebraria* except for the presence of short tracheids with tapering or truncated ends over the transverse side of the rectangular areas.

COMPARISON AND DISCUSSION

Surange and Maheshwari (1962) described a new species *V. raniganjensis*, with xylem differing specifically from that of *V. indica* as described by Walton and Wilson (1932), Pant (1956), and Sen (1958). Surange and Maheshwari (1962) assumed that Royle's type specimen of *V. indica*, No. V. 4189 in British Museum (Natural History) was without carbon. However, since one of us (D. D. P.) had examined Royle's type of *V. indica* and seen carbon in it, we obtained through the courtesy of Dr. Pettitt a small pull from Royle's type. Therefrom, we have been able to confirm that it shows exactly the same kind of xylem as has been described by Walton and Wilson (1932), Pant (1956), Sen (1958), and by us here from other specimens assignable to *V. indica*. This xylem is also similar to that of Surange and Maheshwari's *V. raniganjensis*.

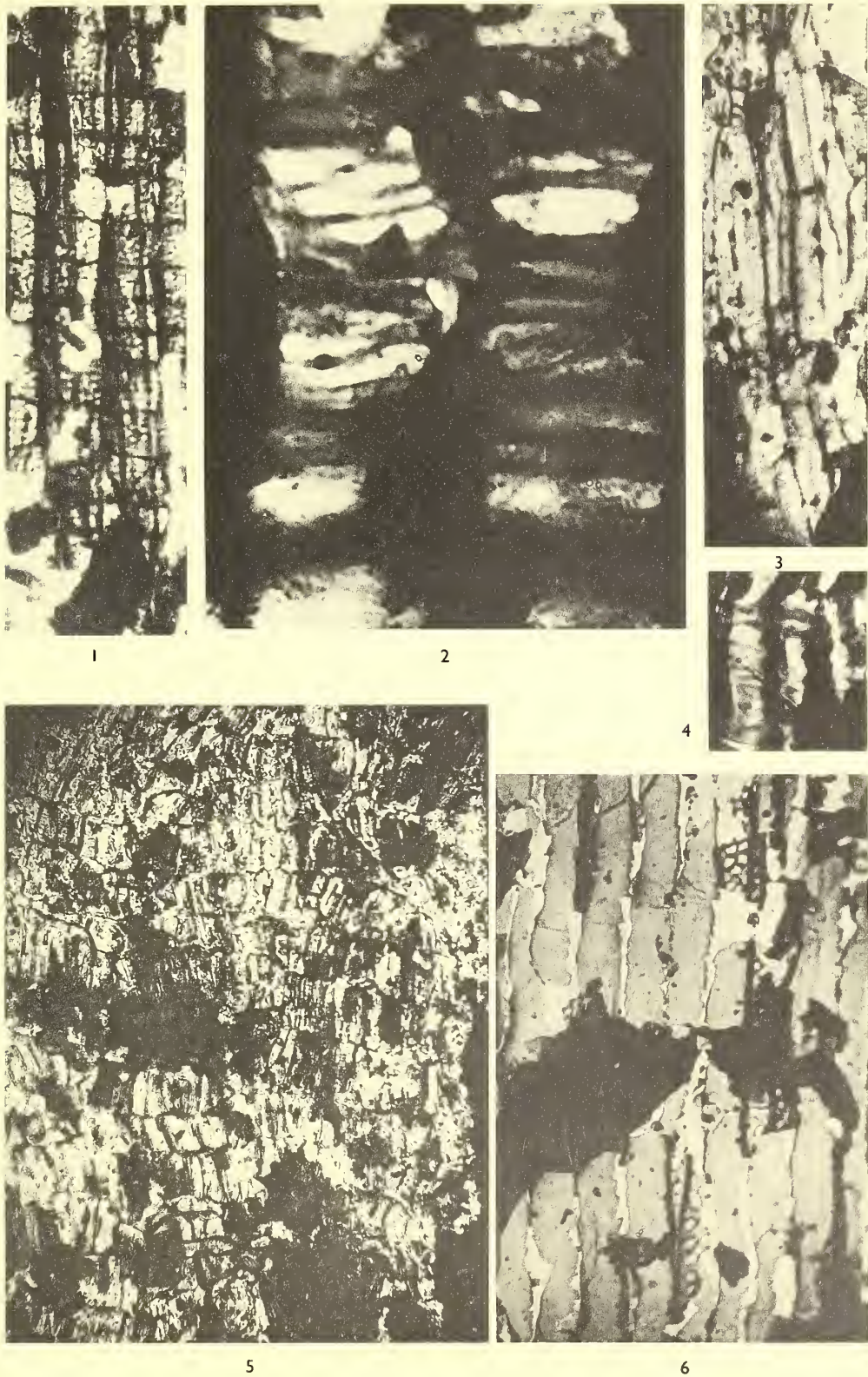
Surange and Maheshwari described the following peculiarities of the xylem of *V. raniganjensis*:

- (a) The pits are 'often' six seriate.
- (b) The pits are 'more than often' arranged irregularly and in groups of 2 to 9 which are sometimes of stellate shape.
- (c) 'Xylem rays if not common are also not scarce as in *V. indica*'. They are usually 1–5 cells high, rarely up to 8 cells high.
- (d) Crossfield pits are 7–9 in number, bordered and with an oval pore and some fields show no pits.
- (e) Absence of large parenchyma cells.

They did not, however, mention the frequency of tracheids with six seriate or irregularly arranged pits or of the xylem rays. The frequent occurrence of irregularly pitted

EXPLANATION OF PLATE 127

Figs. 1–6. *Vertebraria indica* Royle. 1, Xylem showing 13-cell-high ray, Slide No. 1777B, $\times 150$. 2, Xylem showing horizontally elongated, simple oval pits in crossfields, Slide No. 1809 Ba, $\times 800$. 3, Pull showing thin-walled phloem-like cells, Slide No. 1767A, $\times 300$. 4, Portion of tracheid showing scalariform pits, Slide No. 586, $\times 350$. 5, Pull showing broad parenchyma cells, tending to be in radial series, Slide No. 1781C, $\times 40$. 6, Portion of xylem showing unpitted tangential walls, Slide No. 1789C, $\times 230$.



elements of xylem and the occurrence of six seriate tracheids (even though rare) in axes whose xylem is otherwise exactly like that of *V. indica* suggests that such tracheids may not be used to distinguish another species. The frequency of rays in *V. indica* is rather variable. Calculated on the basis of figures and photographs given by Walton and Wilson (1932), Pant (1956), and Surange and Maheshwari (1962), the frequency of rays in the axes described by these authors is within the range determined for *V. indica*. As mentioned above we believe that there is an error in the description of crossfield pits by Walton and Wilson and by Surange and Maheshwari. The only remaining difference is the absence of large parenchyma cells in *V. raniganjensis* and their presence in *V. indica*; however, the negative evidence of the absence of such cells in a pull may be misleading for even in two pulls of the same axis, such cells are often seen to be preserved in some regions and not in other portions. We have also re-examined Pant's original pulls of *V. indica* from Mhukuru coalfield, Tanganyika, and they show the same kind of the xylem as the type. Accordingly we are convinced that axes described as *V. raniganjensis* and *V. indica* belong to the same 'species'.

Surange and Maheshwari (1962) described another new species, *V. myelonis*, which differed from *V. indica* in having a pith in the centre of the axes but no parenchymatous tissue was recorded in the 'pith' region. None of our pulls from the Raniganj and Giridih coalfields shows any trace of a parenchymatous pith although the xylem and parenchyma cells are usually well preserved. Surange and Maheshwari based their species on a single specimen which does show a narrow space (pith) in the centre between the two lateral series of rectangular areas, but they did not describe any parenchyma from this region and the space possibly represents the width of the solid central part of the xylem because we have actually observed solid xylem in this region in numerous specimens and also in the centre of vertically preserved axes. In the absence of any positive evidence of a pith it would be simpler, if this species too is regarded as a synonym of *V. indica*.

MORPHOLOGY OF *VERTEBRARIA*

Structural features

Oldham believed that *Vertebraria* had a solid central core joined to a peripheral bark by a series of radiating longitudinal septa which could be branched (Oldham 1897, pl. 4, fig. 2), and according to his description eight of these septa could usually be seen in a sectional view in vertically preserved axes. He thought that the longitudinal septa were joined at intervals by transverse partitions so that the axes of *Vertebraria* were visualized as having a ring of air chambers around a central solid core. In his view the transverse partitions are responsible for the septate appearance in horizontal preservation. Zeiller (1896) thought that *Vertebraria* axes had an externally ridged form with transverse septa between the longitudinal ridges as in the rhizomes of the living fern *Struthiopteris*.

Both Oldham and Zeiller agreed in regarding the rectangular areas as representing empty spaces (internal or external). Walton and Wilson (1932), however, suggested that the axes of *Vertebraria* had a rayed stele practically without a pith; each carbonaceous ray in a vertically preserved *Vertebraria* was formed by compression of compact secondary xylem having uniseriate parenchymatous rays between its tracheids. These rays of xylem were joined with adjacent xylem rays on either side; rock-filled spaces

(bays) between the carbonaceous rays were not empty but originally occupied by a soft tissue. Pant (1956) agreed with Walton and Wilson on the basis of his study of a *Stigmaria* with rays similarly preserved, and he described large parenchyma cells which occupied the bays.

An interpretation of the features of *Vertebraria* which is similar to that given earlier by Oldham has recently been given by Plumstead (1962), but she agrees with Walton and Wilson (1932) in believing that the chambers were filled with a soft tissue. However, her reconstruction visualizes a solid 'central column communicating by means of large oval cavities with the rest of the axis', and also a woody bark. Recently, Schopf (1965) has generally confirmed the reconstructions of the structural features of *Vertebraria* suggested by Walton and Wilson (1932).

Our investigation of the extensive new material of *Vertebraria* is fully consistent with the views of Walton and Wilson (1932). Pulls from rays of carbon in vertically preserved axes show the same kind of xylem as the surface of the rectangular areas in horizontally compressed axes. Celloidin pulls of carbon from rectangular areas of horizontally preserved axes show tracheids which tend to be short, wide, and curved near the transverse portions but elsewhere the tracheids run uniformly in the longitudinal direction. We have also confirmed that the transverse connections joining adjacent carbonaceous rays are also formed by xylem. As already described by Pant (1956) xylem and phloem over rectangular areas is often overlapped by large parenchyma cells, which are clearly the remnants of a soft tissue which originally filled the bays. The absence of rectangular areas in thinner branches of *Vertebraria* leads us to the conclusion that the parenchymatous bays may have been formed after secondary growth as in the axes of some modern lianas like *Aristolochia*. This may also explain the regular seriated arrangement of the large parenchyma cells.

Stem or root

Vertebraria has been generally recognized as the stem or rhizome of *Glossopteris* after Zeiller (1896) and Oldham (1897) described axes showing apparent attachment of *Glossopteris* leaves, and an axis described by Dolianiti (1954) seemingly confirms this. On the contrary *Glossopteris* bearing axes of *Glossopteris* described by Etheridge (1894), Seward (1910), and Walton and Wilson (1932), do not show any *Vertebraria* features. An explanation for this inconsistency has been offered by Arber (1905) and Pant (1956, 1962) who suggest that the features of *Vertebraria* are only those of its vascular cylinder and accordingly axes where the peripheral tissues are intact would appear different. Walton and Wilson (1932), and Thomas (1952) have, however, doubted the attachment of *Glossopteris* leaves on *Vertebraria* axes.

On the basis of his study of some roots called *Lithorhiza tenuirama*, Pant (1958) suggested by implication that *Vertebraria* could be a root, and pointed out that the roots of *L. tenuirama* could sometimes be found attached to axes of *Vertebraria* and sometimes to axes which combined the features of roots as well as those of a *Vertebraria*. Such axes are somewhat thicker than undoubted roots but thinner than axes showing typical *Vertebraria* features. Roots arise from them endogenously. Unlike roots they show large parenchyma cells characteristic of *Vertebraria* but they entirely lack its rectangular areas. Lately, Schopf (1965) has strongly supported the root nature of *Vertebraria* on the basis of a petrified axis. In this connection he emphasizes the lack of leaf traces or

nodes by *Vertebraria* axes and also the endogenous insertion of its roots (but adventitious roots in stems are also endogenous). However, *Vertebraria* axes are sometimes dichotomised or trichotomised like stems or adventitiously branched roots, although Pant (1958) has also described some similarly forked roots. Pant (1967) has recently described a number of axes lacking rectangular areas of *Vertebraria* type but showing attached leaves of *Glossopteris* and this may also serve as a negative evidence favouring the root character. An investigation of the structural features of *Glossopteris* bearing stems which appear to differ from *Vertebraria* axes may help in solving the problem.

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DIVYA DARSHAN PANT

R. SHANKER SINGH

Department of Botany,

The University, Allahabad, India

THE GRAPTOLITE ASSEMBLAGES AND ZONES OF THE BIRKHILL SHALES (LOWER SILURIAN) AT DOBB'S LINN

by P. TOGHILL

ABSTRACT. The graptolite assemblages and lithologies of the Birkhill Shales (Lower Silurian) at Dobb's Linn are described. The condensed 141 ft. (43 m.) euxinic sequence is divided into eight graptolite zones in descending order: *Rastrites maximus*, *Monograptus sedgwickii*, *M. convolutus*, *M. gregarius*, *M. cyphus*, *Cystograptus vesiculosus*, *Akidograptus acuminatus*, and *Glyptograptus persculptus*. These zones are compared with the original work of Lapworth (1878), and with equivalent zones elsewhere in Great Britain. The base of the Middle Llandovery at the type locality for the graptolitic Llandovery (Valentian) is taken at the base of the *gregarius* Zone (*triangulatus* Zone in Wales), and not at the base of the *maguus* Zone, as is the current practice in Wales.

THE classic locality of Dobb's Linn, and the surrounding Moffat area, have been left relatively untouched by research workers since the admirable account of Lapworth (1878).

Because of the lack of new information from the Moffat area, recent reviews of Southern Uplands geology (Walton 1963, 1965) have had to discuss the Llandovery geology of the area using information obtained in, and unaltered since, the late 1800s, and thus their discussions are rather speculative. The present work does not, however, suggest any major errors by Lapworth. It is only the application of knowledge obtained since 1878 which has allowed alterations and additions to his classic results. The foundation for a Llandovery graptolite zonal scheme was laid down by Lapworth (1878, 1880), and his original research was quickly followed up in the Lake District by Marr and Nicholson (1888). Table 2 is a correlation of the large number of zonal schemes which have been used in Great Britain for the Llandovery (Valentian) up to the base of *turriculatus* Zone. The most recent scheme given by Curtis (1961) is in fact a compilation of most zones recognized in Wales, and based on the original research of O. T. Jones (1909), and Jones and Pugh (1916, 1935). The present work reappraises the graptolite fauna of the condensed 141 ft. (43 m.) euxinic Birkhill Shale sequence at the type locality, redefines the Llandovery graptolite zones exposed at Dobb's Linn, and compares them with equivalent zones elsewhere. The condensed sequence at Dobb's Linn is almost completely fossiliferous and thus is the most suitable place to define Llandovery graptolite zones, not only because it is the type locality for the graptolitic Llandovery (Valentian) but also because the equivalent sequence in Wales is a thick series (1,000 ft.) of coarse sediments in which the graptolite horizons are separated by considerable thicknesses of unfossiliferous strata (Jones 1909, p. 504).

POSITION OF SECTIONS

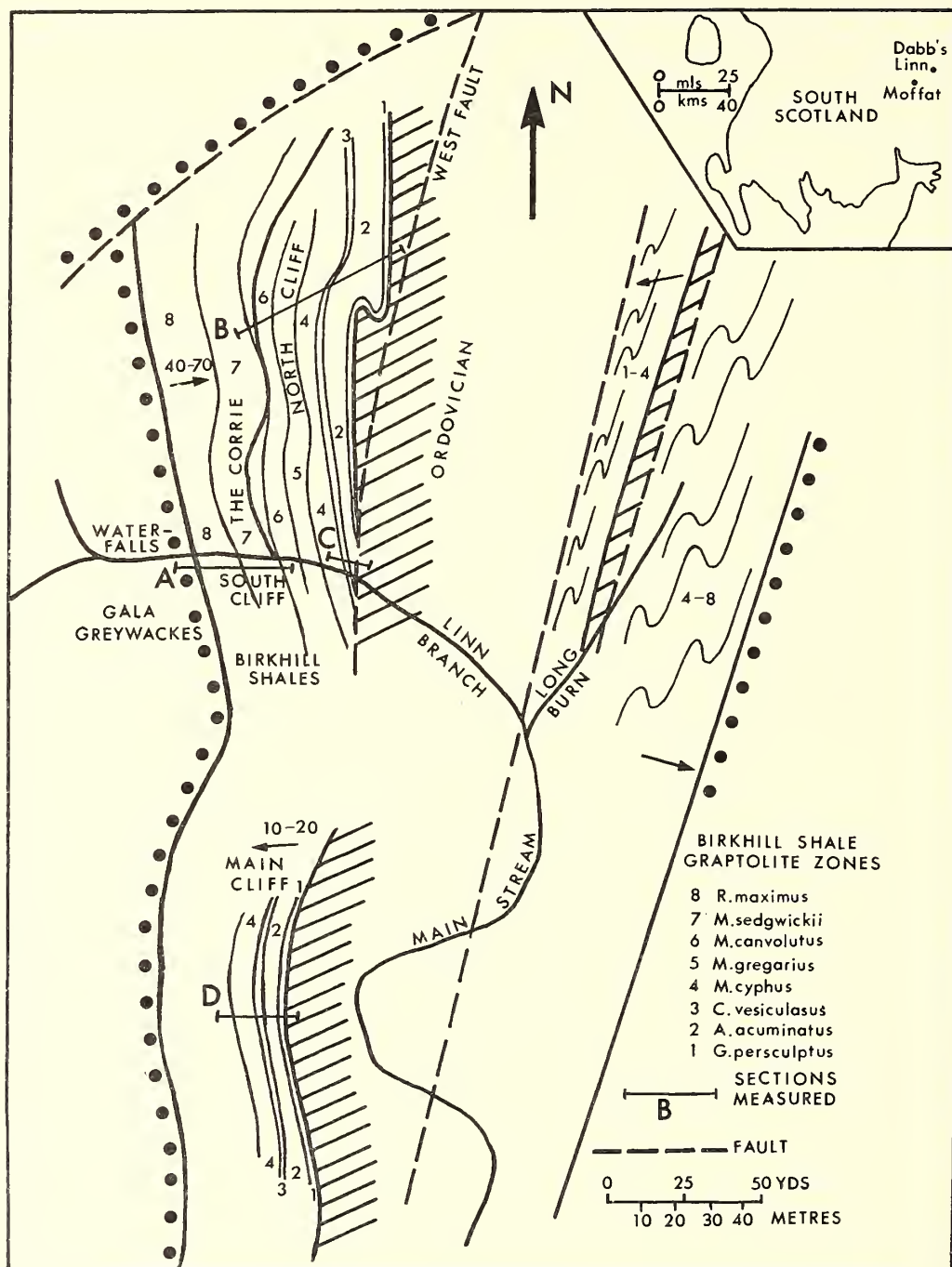
Dobb's Linn lies 10 miles north-east of Moffat, and at the head of the Moffat Water. A complicated isoclinal fold structure, with Caledonoid trend, brings the graptolitic condensed sequence of Moffat Shales (Caradoc-Llandovery) to the surface from below

the overlying Gala Greywackes (Upper Llandovery). This work is only concerned with the highest (Birkhill) division of the Moffat Shales, from the base of the Silurian (*persculptus* Zone) up into the *maximus* Zone of the Upper Llandovery.

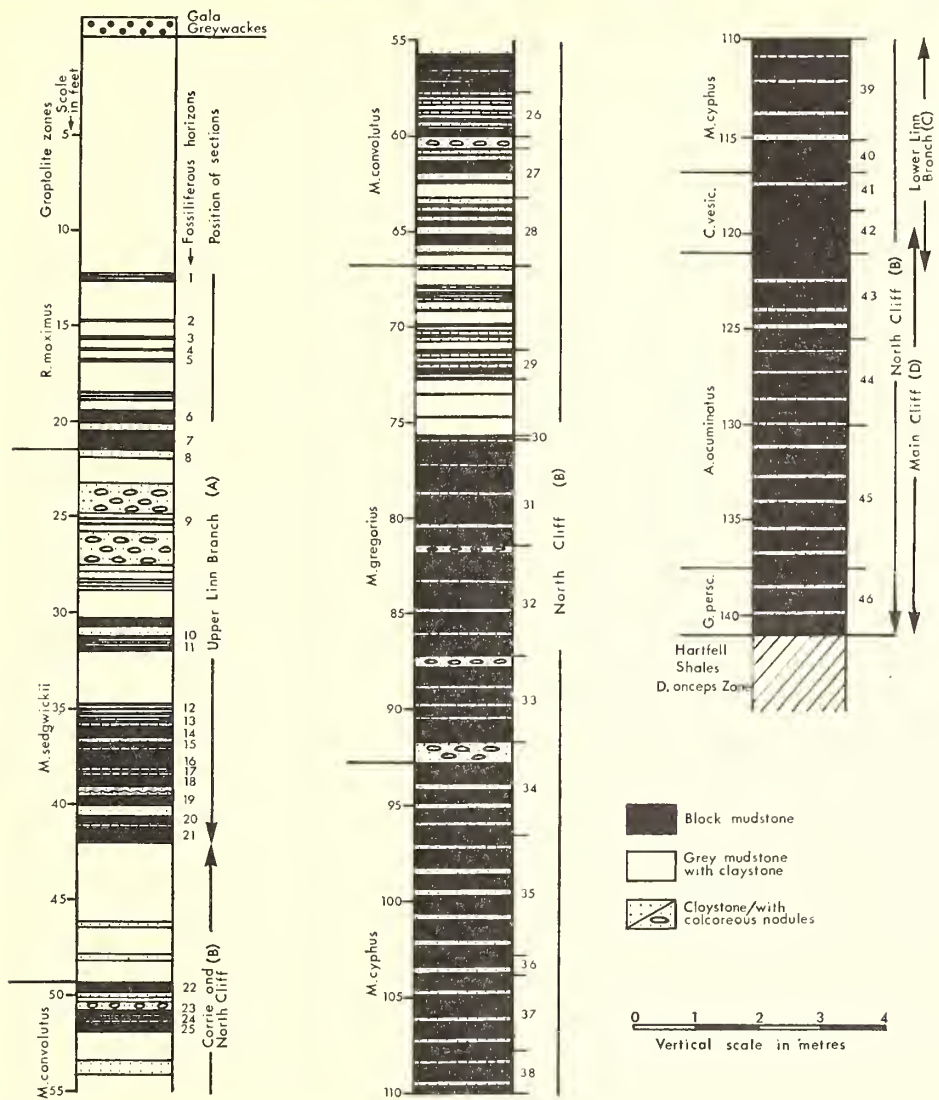
The south-east limb of the fold is highly contorted and no detailed measurements are possible. The north-west (inverted) limb however shows an excellent section of the Birkhill Shales, particularly in the Linn Branch, and on the North and Main Cliffs (text-fig. 1). A large waterfall has developed in the Linn Branch at the junction of Gala Greywackes and Birkhill Shales, and below this all but the lowest beds of the Birkhill Shales are exposed, the beds being inverted and dipping downstream at between 40° and 70°. The basal beds are cut out by a strike fault, and there is also a considerable amount of strike faulting in the *convolutus*, *gregarius*, and upper *cyphus* Zones. The Corrie and North Cliff show a continuous section from the lower *sedgwickii* Zone down to the base of the Silurian with little or no strike faulting. The Main Cliff (text-fig. 1) provides an excellent section across the Ordovician-Silurian boundary, and is by far the best place for measuring up the basal beds of the Birkhill Shales. Using these sections a detailed lithological sequence (text-fig. 2) has been worked out for the Birkhill Shales. Descending from the Gala Greywackes, the *maximus* and *sedgwickii* Zones have been measured up in the Upper Linn Branch (section A, text-fig. 1). Conspicuous lithological horizons in the lower *sedgwickii* Zone then allowed the section to be transferred to the Corrie and North Cliff (section B, text-fig. 1) where the remainder of the sequence was measured down to the base of the *persculptus* Zone. The lower part of the North Cliff section (*persculptus* to *cyphus* Zones) was correlated with, and supplemented by, collections from the Lower Linn Branch section (C) in the *cyphus*, *vesiculosus* and upper *acuminatus* Zones, adjacent to the West Fault, and the Main Cliff section (D) in the *persculptus*, *acuminatus* and *vesiculosus* Zones.

THE LITHOLOGIES OF THE BIRKHILL SHALES

Three main lithological types are present: massive black pyritic graptolitic mudstone, massive barren grey mudstone, and beds of soft, pale grey to orange, clay-like deposits. Lapworth (1878) referred to this latter conspicuous lithology under a variety of names including, 'white clay bands', 'soft shaly clay', and 'white lines', but the term claystone has recently been applied to these deposits by Walton (1965, p. 185). These beds, which often contain lines of calcareous nodules, weather out very easily and may be of volcanic origin (Walton 1963, pp. 85, 89; 1965, p. 185). This lithology makes up a large proportion of the Birkhill Shales and also occurs in the underlying Hartfell Shales, and persists into the Gala Greywackes. If volcanic in origin it indicates a period of vulcanicity from the Caradoc into the Upper Llandovery. The lower 65 ft. of the succession is made up of alternations of black mudstone and pale soft claystone, with occasional nodule bands, but without any grey mudstone at all. These lower Birkhill Shales follow directly on top of grey mudstones of the Hartfell Shales. The black mudstones are generally between 3 in. and 1 ft. thick and the intervening claystones are usually between 1 in. and 3 in. thick, but occasionally up to 1 ft. Within the upper *acuminatus*, *vesiculosus*, and lower *cyphus* Zones is a conspicuous 10-ft. thickness of massive black mudstone with very few claystones. These massive beds, Lapworth's *vesiculosus* Flags, are a conspicuous unit of the lower Birkhill Shales well exposed in the Lower Linn Branch. The upper 76 ft. of



TEXT-FIG. 1. Locality map of Dobb's Linn, showing position of sections.



TEXT-FIG. 2. Vertical section through the Birkhill Shales, showing the position of fossiliferous horizons, etc. Although an attempt has been made to indicate the frequency of claystones, the section is diagrammatic, particularly below 55 ft. The positions of all nodular claystones, and of individual fossiliferous beds above 55 ft. are precise.

the Birkhill Shales is made up of alternations of grey and black mudstones, varying in thickness from mere bedding plane bands to beds of 1 ft., and many soft claystones with occasional nodule bands. The inter-relationships of grey and black mudstones are shown in text-fig. 2. The highest graptolitic horizons in the Birkhill Shales (*maximus* Zone) occur as thin bands $\frac{1}{8}$ in. to 1 in. thick in a dominantly grey mudstone sequence. About 12 ft. above the highest black band the first greywacke appears in the Upper Linn Branch,

below the waterfall. It is 6 in. thick and is taken as the base of the Gala Greywackes, as indicated by Lapworth (1878, p. 322). This bed is followed by 14 ft. of massive grey mudstones, thin greywackes, and claystones, before the massive greywackes at the base of the waterfall are reached.

From the above description, and from text-fig. 2, it can be seen that within the Birkhill Shales there is a gradual change from the exclusively euxinic facies of the lower Birkhill Shales, through the grey and black mudstones of the *convolutus* and *sedgwickii* Zones, into the dominantly grey mudstones of the *maximus* Zone, and finally into greywacke facies. Throughout the Moffat area the base of the Gala Greywackes has been found to be highly diachronous, and this will be further explained when describing the fauna of the *R. maximus* Zone.

THE CHARACTERISTIC GRAPTOLITE FAUNA OF THE BIRKHILL SHALES

The various graptolite zones have been divided up into fossiliferous horizons (1–46) which are indicated on text-fig. 2. The detailed fauna of any horizon can be ascertained from Table 1.

Zone of Glyptograptus persculptus

This zone is well exposed on the Main Cliff (section D, text-fig. 1), but is less accessible at the top of the North Cliff (base of section B). On the Main Cliff the black mudstones of the Birkhill Shales follow barren grey mudstones of the *anceps* Zone of the Hartfell Shales. The highest fossiliferous band with *D. anceps* is approximately 10 ft. below the base of the Birkhill Shales. The *persculptus* Zone (horizon 46, text-fig. 2) comprises $3\frac{1}{2}$ ft. (1.06 m.) of black mudstone with thin claystones. The mudstones are often weathered to a drab grey colour and the fauna is then extensively destroyed. At the base of the zone is a 4-in. bed crowded exclusively with *Climacograptus scalaris normalis*. The remainder of the zone is characterized by this species with the zone fossil, and *Climacograptus medius*, *C. scalaris miserabilis* and *Diplograptus modestus s.l.*

Zone of Akidograptus acuminatus

$16\frac{1}{2}$ ft. (5.0 m.) of black mudstones with many thin claystones are assigned to this zone (horizons 43–5). It is best exposed on the Main Cliff (section D), but the highest beds are well exposed in the Lower Linn Branch (section C). The whole zone is exposed on the North Cliff (section B) but is rather inaccessible. The lower part of the zone weathers in a similar fashion to the *persculptus* Zone, but the highest beds are hard and massively bedded, and form the lowest part of Lapworth's *vesiculosus* Flags.

The base of the zone is marked by the appearance of *Akidograptus* and the zone is characterized by *A. acuminatus s.l.* and *A. ascensus*, neither of which occur outside the zone. The latter occurs commonly before the main burst of *A. acuminatus*, which commences in the middle of the zone. *Glyptograptus persculptus* is common in the lower part and *Climacograptus trifilis* in the middle of the zone. *Cystograptus vesiculosus* appears in the middle and is common at the top of the zone, and *Diplograptus modestus* occurs throughout. *Climacograptus scalaris normalis* and *C. medius* are common throughout, and *C. rectangularis* appears in the upper part.

Zone of Cystograptus vesiculosus

This zone is represented by 4 ft. 3 in. (1.3 m.) of massive black mudstone with a few claystones (horizons 41–2), and is best exposed in the Lower Linn Branch (section C). The base is marked by the most conspicuous horizon in the whole of the Silurian, the appearance of the Monograptidae, together with *Dimorphograptus* and *Rhaphidograptus*. The zone is characterized by the earliest monograptids, with the zone fossil, and dimorphograptids with long uniserial portions: *D. elongatus* and *R. extenuatus*. One particular bedding plane at the base of the zone is crowded with *Monograptus cyphus praematurus* Toghill (1968), which with *M. atavus* Jones is the earliest monograptid. The latter is common throughout the zone and occurs in the upper part with *M. acinaces* and *M. incommodus*. *Climacograptus innotatus* appears at the base of the zone and occurs throughout as does *Diplograptus modestus* s.l. *Glyptograptus tamariscus* s.l. appears and climacograptids are abundant including *C. medius*, *C. rectangularis*, and *C. scalaris normalis*.

Zone of Monograptus cyphus

This zone is represented by 24 ft. (7.3 m.) of massively bedded black mudstones with yellow and orange claystones, which are rare towards the base. The zone (horizons 34–40) has been measured up in the Lower Linn Branch (section C) and on the North Cliff (section B). The higher parts of the zone in the Lower Linn Branch are extensively strike-faulted. The overlying *gregarius* Zone has at its base a most conspicuous 1 ft. claystone with large calcareous nodules, and this, the lowest nodular claystone, is well exposed on the North Cliff.

At the base of the zone dimorphograptids with short uniserial portions appear, including: *D. confertus*, *D. confertus swanstoni*, *D. erectus*, *D. decussatus* s.l., and *D. longissimus*. Of these the first three are the commonest, and the first two persist into the upper parts of the zone. *D. physophora* is rare but probably occurs throughout as does *Rhaphidograptus toernquisti*. *Monograptus cyphus* is rare at the base of the zone but soon becomes abundant and ranges throughout the zone as do *M. sandersoni*, *M. incommodus*, *M. atavus*, and *M. acinaces*. *M. gregarius* and *M. revolutus* appear in the middle of the zone and are common at the top. *Cystograptus vesiculosus* and *Climacograptus innotatus* are limited to the basal beds where the latter is common. *Climacograptus medius* and *C. rectangularis* are abundant in the lower part of the zone, but do not reach the top, and neither does *C. scalaris normalis*. *Glyptograptus tamariscus* s.l. occurs throughout the zone.

Zone of Monograptus gregarius

26 ft. (7.9 m.) of strata are assigned to this zone (horizons 29–33) as measured on the North Cliff (section B). Black mudstones with thick nodular claystones occupy the lower 18 ft. but these grade upwards into banded grey and black mudstones with many claystones.

The base of the zone is marked by the appearance of *Monograptus triangulatus* s.l. which occurs throughout the zone and is particularly common in the lower part. *M. gregarius* and *M. revolutus* occur throughout the zone, but *M. sandersoni*, *M. incommodus*, and *M. atavus* are limited to the lower part. *M. communis* is characteristic of the upper part of the zone, and *Rastrites longispinus* and *R. peregrinus* appear in the middle.

A conspicuous horizon (30) 8 ft. from the top of the zone yields abundant specimens of *Monograptus fimbriatus* with many petalograptids, including *Petalograptus minor*, *P. palmeus latus*, *P. palmeus ovato-elongatus*, as well as a few specimens of *Diplograptus magnus*. This is the only horizon with *D. magnus* and *M. fimbriatus*, and the main burst of the latter occurs above that of *M. triangulatus s.l.*, as suggested by Sudbury (1958). This horizon is presumably equivalent to the *magnus* Band in Wales, although here it is only 3 in. thick. The unfossiliferous beds (text-fig. 2) which overlie horizon 30 but underlie the highest fossiliferous horizon (29) of the *gregarius* Zone might be considered part of the *magnus* Zone. This 3-ft. thickness of beds compares with 27 ft. assigned to the *magnus* Zone in Wales, although there the actual *magnus* Band at the base is only 6 in. thick (Jones and Pugh, 1935, p. 275), the remainder of the zone being relatively unfossiliferous.

In horizon 29 *Monograptus leptotheca* is common, *M. denticulatus* appears, and this is the only horizon with *M. argenteus*. It can be equated with the *argenteus* Zone of the Lake District (Marr and Nicholson 1888), and the *leptotheca* Zone of Wales, which are here considered to be equivalent. *M. argenteus* in abundance seems to be restricted to the Lake District, its place in Wales and Scotland being taken by *M. leptotheca*.

Zone of Monograptus convolutus

The foot of the North Cliff (section B) provides an excellent section of this zone (horizons 22–8) which is $17\frac{1}{2}$ ft. (5.35 m.) thick and made up of two groups of highly fossiliferous black mudstones with claystones separated by barren grey mudstones and claystones (text-fig. 2). The upper group of fossiliferous beds (horizons 22–5) is, in fact, Lapworth's original *clingani* Band, and the lower group his *cometa* Zone. The detailed fauna of any horizon can be ascertained from Table 1.

Faunally the base of the zone is marked by the appearance of *Monograptus lobiferus* in abundance, with *M. convolutus*. The former is limited to the basal beds of the zone but the latter persists, with *M. clingani*, throughout the zone and is found as high as the lower *maximus* Zone. *M. triangulatus*, *M. communis*, and *M. leptotheca* are all present in the basal beds, but *M. gregarius* has disappeared. Cephalograptids, and petalograptids with protracted proximal ends are characteristic including in the lower part, *Petalograptus folium* and *Cephalograptus tubulariformis*, and *C. cometa* in the upper part of the zone. Rastritids are common and include *R. hybridus*, *R. peregrinus*, *R. longispinus*, and *R. approximatus geinitzi*. In the higher group of black mudstones the following monograptids are common: *M. clingani*, *M. limatulus*, *M. crenularis*, *M. convolutus*, and *M. decipiens*, together with *Cephalograptus cometa*, *Glyptograptus tamariscus incertus*, and *Orthograptus bellulus*. Of these species *M. crenularis* is very typical of the upper *convolutus* Zone.

Zone of Monograptus sedgwickii

$27\frac{1}{2}$ ft. (8.4 m.) of strata are assigned to this zone (horizons 8–25) which is best exposed in the Upper Linn Branch (section A), and the Corrie under the North Cliff (section B). Lithologically the zone can be divided into three units. A lower 7 ft. of barren grey mudstones with claystones, best seen in the Corrie; a middle 6 ft. of fossiliferous black mudstones with claystones (horizons 14–21) exposed in the Corrie and Upper Linn Branch; and an upper $14\frac{1}{2}$ ft. of grey mudstones with claystones and a few fossiliferous

[illegible]

TABLE 1. The vertical distribution of the Graptoloidea in the Birkhill Shales at Dobb's Linn.

black seams (horizons 8–13) exposed in the Upper Linn Branch. The middle unit is characterized by an abundance of *Monograptus sedgwickii*, *M. regularis*, and *M. jaculum*, with triangulate monograptids in the lower part, including *M. convolutus*, *M. involutus*, and *M. decipiens*. Glyptograptids are common and *Petalograptus palmeus tenuis* occurs with *Climacograptus scalaris*. The upper 14½ ft. contain a similar but poorer fauna in which *M. spiralis* and *M. attenuatus* appear.

Zone of Rastrites maximus

The highest 21½ ft. (6.55 m.) of the Birkhill Shales is assigned to this zone. Grey mudstones and claystones predominate, and grade up into the Gala Greywackes, the base of which is taken at the first greywacke seen in the Upper Linn Branch (section A), as indicated by Lapworth (1878, p. 322). Black mudstones are restricted to the lowest 9 ft. Seven separate fossiliferous horizons occur, and of these the two lowest yield a large fauna (Table 1). In these basal beds *Monograptus sedgwickii*, *M. regularis*, *M. nudus*, *M. convolutus*, and *M. circularis* are common, but the latter two species only occur commonly on one particular bedding plane. These common species occur with *M. spiralis*, *M. attenuatus*, *M. gemmatus*, *M. decipiens*, *M. intermedius*, *Climacograptus extremus*, and *Petalograptus palmeus tenuis*. At this lower level *Rastrites maximus* and *M. halli* are rare.

The highest fossiliferous horizon of the Birkhill Shales at Dobb's Linn is a 4-in. composite band of four black mudstones up to 1 in. thick separated by thin claystones. It yields *Rastrites maxinus*, *R. fugax*, *R. linnaei*?, *R. distans*?, *R. hybridus*, *Monograptus halli*, *M. sedgwickii*, *M. convolutus*, *M. spiralis*, and *M. intermedius*.

Owing to the diachronism of the overlying Gala Greywackes (see below), higher horizons not represented by fossiliferous strata at Dobb's Linn, but occurring south east of the Caledonoid strike line through Dobb's Linn, are characterized by the following common species: *Rastrites maximus*, *Monograptus halli*, and *M. spiralis*, with *M. runcinatus*, *M. nudus*, and *M. turriculatus minor*.

THE LLANDOVERY GRAPTOLITE ZONES AT DOBB'S LINN

The graptolite zonal scheme used here has been arrived at by considering the original scheme of Lapworth (1878, 1880), as modified by Elles and Wood (1913), and the large number of schemes erected in Wales by Jones (1909), Jones and Pugh (1916), Davies (1926), and others, as summarized by Curtis (1961). Table 2 shows an attempted correlation between the zones used here, and other schemes used elsewhere.

The *Glyptograptus persculptus* Zone was defined at Dobb's Linn for the first time by Toghill (1968), although the species was first recorded from there by Davies (1929). The validity of the zone is emphasized by the absence of *Akidograptus*, which does not appear until the overlying *acuminatus* Zone.

The *Akidograptus acuminatus* Zone as defined here is approximately the same as defined by Lapworth (1878, pp. 250, 252, 318–20), although the basal beds have been separated off as the *persculptus* Zone.

The base of the *Cystograptus* [*Orthograptus*] *vesiculosus* Zone has been taken at the incoming of the monograptids, as suggested by Elles (1925, p. 344). The restricted thickness (4 ft. 3 in.) used here is only the lower part of the zone as originally

defined by Lapworth (1878, pp. 250, 252, 319–20), but the zone has been strictly defined on the ranges of the earliest monograptids, as given by Elles (1925), and dimorphograptids. The fact that the zone is so thin compared with the 16 ft. assigned to it by Lapworth is due to the more precise fixing of monograptid ranges, particularly those of *M. cyphus*, *M. sandersoni*, *M. incommodus*, and *M. atavus*. Lapworth (1878, p. 319) did not give a very detailed monograptid fauna from his *vesiculosus* Zone and lower *gregarius* Zone, recording only *M. 'tenuis'* and *M. attenuatus* from the *vesiculosus* Zone, and of course *M. incommodus* and *M. atavus* were not described until later. Elles (1925) did not give any thicknesses for the *vesiculosus* Zone, and thus this is the first time that the zone has been defined at Dobb's Linn (the type locality) using a comprehensive monograptid fauna. The monograptid ranges agree with Elles's definition of the zone (1925), but she recorded *Dimorphograptus confertus* and *D. confertus swanstoni* as being characteristic of the *vesiculosus* Zone. These are here taken as indicating the base of the overlying *cyphus* Zone together with the appearance of *M. cyphus* and *M. sandersoni*.

Thus, the *vesiculosus* Zone as used here is only the lower part of the zone as defined by Lapworth (1878), Elles and Wood (1913), and Elles (1925). It is probably equivalent to the *atavus* Zone in Wales (Jones 1909, Curtis 1961). The *cyphus* Zone includes the remainder of Lapworth's *vesiculosus* Zone and part of his *gregarius* Zone. It is equivalent to the *cyphus* and *acinaces* Zones in Wales (Jones, 1909). From Table 1 it can be seen that the ranges of *M. atavus* and *M. acinaces* are almost identical, the former having the larger range, and the latter occurs, in the later part of its range, with *M. cyphus*. Although the *vesiculosus* Zone as defined here is equivalent to the *atavus* Zone in Wales, the former title is preferred on historical grounds, Dobb's Linn being the type locality.

The *M. gregarius* Zone as defined here is equivalent to the *triangulatus*, *magnus*, and *leptotheca* Zones in Wales (Curtis, 1961). The base is taken at a conspicuous faunal horizon, the appearance of triangulate monograptids, and is probably the base of Lapworth's Upper Division of his *gregarius* Zone (1878, pp. 319, 321), where he records *M. triangulatus* 'in profusion'. The main horizon (29) with *M. leptotheca* is only 1 ft. thick, and that (30) with *Diplograptus magnus* only 3 in. thick. The former horizon contains *M. argenteus* and is presumably equivalent to the *argenteus* Zone in the Lake District. *M. triangulatus s.l.* ranges right through the *gregarius* Zone as defined here as does the zone fossil, and the title *gregarius* Zone is preferred on historical grounds, although it must be noted that it is equivalent to the *triangulatus s.l.* Zone of W. D. V. Jones (1945). Jones and Pugh (1935, pp. 275, 276) stated that the *magnus* Zone was made up of 27 ft. of mainly unfossiliferous strata with a 6-in. *magnus* Band at the base. Similarly the *leptotheca* Zone was given as 20 ft. of relatively unfossiliferous beds with a 2½-ft. *leptotheca* Band at the base. The practice of erecting zones based on thin graptolite bands separated by barren strata is not considered correct, particularly as one has no idea of the fauna of the intervening beds. Although the horizons with *M. leptotheca* and *Diplograptus magnus* at Dobb's Linn provide direct correlation with the sequence in Central Wales, they should only be regarded as bands and not zones.

Dr. R. B. Rickards records (*in litt.*) that the lithologies and faunas at the level of the *gregarius* Zone in the Howgill Fells (eastern Lake District) are very similar to Dobb's Linn. He recognizes the three zones *triangulatus*, *magnus*, and *argenteus* (*leptotheca*), and reports that there is a marked lithological change from black to grey mudstones at the level of the *magnus* Zone, a state of affairs comparable with the sequence at Dobb's Linn

where the first grey mudstones appear immediately above the 3-in. band with *Diplograptus magnus*.

The *M. convolutus* Zone as used here is equivalent to the same zone as defined by Elles and Wood (1913), and Elles (1925), the *cometa* Band being included in the zone. In some cases, in Wales, the *cometa* Band has been treated as a separate zone (Jones, 1909, 1929; Curtis, 1961). The zone is equivalent to the *cometa* Zone of Lapworth (1878, pp. 322-3) together with the *clingani* Band of his *sedgwickii* Zone.

The base of the *M. sedgwickii* Zone as defined here is equivalent to the same horizon in Wales, being taken at the appearance of *M. sedgwickii*. The *clingani* Band of Lapworth's *sedgwickii* Zone has been relegated to the *convolutus* Zone.

The base of the *Rastrites maximus* Zone has been taken at a similar level to Lapworth (1878, pp. 322, 325-7), but the two species which according to Lapworth characterize the zone at Dobb's Linn, *R. maximus* and *M. halli*, have not been found to be at all common in the zone, but occur abundantly in localities south-east of Dobb's Linn (see below). The zone is considered to be equivalent to the *halli* Zone in Wales (Jones and Pugh 1916, W. D. V. Jones 1945). Some authors have suggested in the correlation charts of review papers (Jones 1921, 1929; Curtis 1961) that a *maximus* Zone has been defined in Wales above the *halli* Zone. In fact this has never been done, although within the *halli* Zone around Machynlleth (Jones and Pugh 1916) there is a separate *Rastrites* Band above a *halli* Band. The only use of a *R. maximus* Zone in Wales was by Elles (1909) in the Conway area where it lay between the *sedgwickii* and *crispus* Zones.

Localities south-east of the Caledonoid strike-line through Dobb's Linn (Craigmichan Scars, Thirlstane Scar, and Beldcraig Burn) expose fossiliferous horizons which are higher in the *maximus* Zone than any fossiliferous strata at Dobb's Linn. Lapworth compared these sections directly with the *maximus* Zone at Dobb's Linn (1878, pp. 326-7) as if they were exactly the same horizon. He was unaware of the diachronous nature of the Gala Greywackes south-east of Dobb's Linn which meant that their base had 'stepped up' in relation to Dobb's Linn. He was, however, quite aware that the Gala Greywackes 'stepped down' north-west of Dobb's Linn. These localities south-east of Dobb's Linn yield *Rastrites maximus* and *Monograptus halli* in abundance with *M. runcinatus*, *M. spiralis* and rarely *M. turriculatus minor*, and further substantiate the suggestion that the *halli* and *maximus* Zones are equivalent. The latter name should take priority on historical grounds. Higher horizons in the Gala Greywackes south-east of Dobb's Linn yield a fauna which is typical of the *Monograptus turriculatus* Zone, including, *M. exiguus*, *M. barrandei*, *M. nodifer*, and the zone fossil.

THE TERMS LOWER, MIDDLE, AND UPPER LLANDOVERY APPLIED TO THE BIRKHILL SHALES

The terms Llandovery (Murchison 1859) and Valentian (Lapworth 1876) are now considered to be synonymous, and the former term has priority. However, the Valentian is usually considered to be the graptolitic Llandovery, and as the divisions of the Llandovery are based on a shelly fauna and unconformities in the type area (Jones 1925), it is unlikely that the divisions can be readily applied to the graptolitic sequence.

When the Valentian was further defined by Jones (1921) the base was taken at the base of the *G. persculptus* Zone (1921, pp. 173-4), this zone having been originally

defined in the graptolitic sequence of Central Wales (Jones 1909, p. 482). This level is now accepted as the base of the Llandovery (Curtis 1961, p. 129). The base of the Middle Llandovery is usually equated to the base of the *magnus* Zone in the graptolitic sequence of Central Wales (Curtis 1961, p. 130), but this is entirely based on lithological considerations (Jones, 1925, p. 366; 1947, p. 3; 1954, p. 252; Jones and Pugh 1935, pp. 274–5). The only variation from this opinion was by Jones in 1929 when he included the *magnus* Zone in the Lower Llandovery (1929, p. 97). The highest graptolites recorded from the Lower Llandovery at Llandovery are *Monograptus incommodus* and *Climacograptus hughesi* from the top of A4 (Jones 1925, p. 360; 1929, p. 94), and these were considered to indicate the top of the *acinaces* Zone (Jones 1925, p. 360). The Middle Llandovery at Llandovery has yielded *Monograptus decipiens*, *M. cf. lobiferus*, and *M. cf. regularis*. These were collected from near to the top of the division and considered by Jones (1925, p. 366) to indicate the *convolutus* Zone. The abundance of *M. sedgwickii* at 150 ft. above the base of the Upper Llandovery at Llandovery (Jones 1925, p. 370) suggests that the present accepted level for the base of the Upper Llandovery in the graptolitic sequence, i.e. the base of the *sedgwickii* Zone, is quite acceptable. However, there is no such fixed level for the base of the Middle Llandovery in the graptolitic sequence which could, on the evidence stated above, lie as low as the base of the *cyphus* Zone, or even as high as the base of the *convolutus* Zone (Jones 1925, p. 366). This is an unsatisfactory situation, and the problem cannot really be solved until more graptolite evidence is obtained from the Llandovery area, or shelly evidence from the graptolitic sequence. Therefore as the type area cannot offer any faunal evidence which will fix the Lower-Middle Llandovery boundary with any certainty in the graptolitic sequence, there can be no harm in considering the graptolite fauna of the Llandovery (Valentian) as a whole, in order to suggest an equivalent horizon in the graptolitic sequence as a working base for the Middle Llandovery.

Within the graptolite fauna of the Birkhill Shales are four distinct divisions corresponding to those erected by Elles (1922) and further elaborated by Bulman (1958). The lowest part of the Birkhill Shales below the incoming of monograptids (*persculptus-acuminatus* Zones) is equivalent to the Ortho-Climacograptid sub-fauna of Bulman (1958, pp. 170–1), the highest division of Elles's Diplograptid Fauna. The next division of the Birkhill Shales, above the incoming of monograptids, but below the appearance of triangulate monograptids, *vesiculosus-cyphus* Zones, (*atavus-cyphus* Zones in Wales) represents the lowest division, A, of Bulman's Monograptid Fauna. The next division, *gregarius-convolutus* Zones, (*triangulatus-convolutus* Zones in Wales), represents the second division, B, of Bulman's Monograptid Fauna, and the final division, *sedgwickii-maximus* Zones represents part of the third division, C, of the Monograptid Fauna (Bulman 1958, pp. 170–1).

The base of the Llandovery is well fixed in the graptolitic sequence at the base of the *persculptus* Zone, which was defined for the first time in Scotland by Toghill (1968). It is worth noting that Elles (1922, p. 195) suggested that the lowest two zones of the Llandovery (*persculptus-acuminatus* Zones) being devoid of monograptids could well be relegated to the Ordovician on faunistic grounds, but this has never been accepted. The base of the Middle Llandovery if taken at the base of the *magnus* Zone is some way above the appearance of triangulate monograptids, and some way above the base of the *gregarius* Zone as defined here. The appearance of triangulate monograptids at the base

of the *gregarius* Zone (*triangulatus* Zone in Wales) corresponds to the base of the second division, B, of the Monograptid Fauna. It would be more convenient if the base of the Middle Llandovery in the graptolitic sequence were to be taken at the base of the *triangulatus* Zone in Wales, and thus equate with the base of the *gregarius* Zone at Dobb's Linn. If acceptable the base of the Middle Llandovery would then correspond to the base of the second division of Bulman's Monograptid Fauna (Bulman 1958, pp. 170-1). The base of the Upper Llandovery taken at the base of the *sedgwickii* Zone is a convenient horizon as it is the base of the third division of the Monograptid Fauna. Thus the stage boundaries of the Llandovery in the graptolitic sequence would now correspond to significant faunal horizons, though within the Lower Llandovery is the most conspicuous horizon of all, the appearance of the monograptids.

In conclusion, the Lower Llandovery at Dobb's Linn is represented by the zones of *Glyptograptus persculptus*, *Akidograptus acuminatus*, *Cystograptus vesiculosus*, and *Monograptus cyphus*, and is 48 ft. (14.6 m.) thick. The Middle Llandovery includes the zones of *M. gregarius* and *M. convolutus* and is 44 ft. (13.4 m.) thick. Only part of the Upper Llandovery is present, represented by the zones of *M. sedgwickii* and *Rastrites maximus*. These two zones are 49 ft. (15 m.) thick and pass up into the great thickness of the Gala Greywackes which (together with the Hawick Rocks?) represent the remainder of the Upper Llandovery.

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P. TOGHILL
Department of Palaeontology,
British Museum (Nat. Hist),
Cromwell Road,
London S.W. 7

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NUMMULITES (FORAMINIFERA) FROM THE UPPER EOCENE KOPILI FORMATION OF ASSAM, INDIA

by BIMAL K. SAMANTA

ABSTRACT. Four species of *Nummulites* are described and illustrated from the Kopili Formation, Garo Hills, Assam, India. This is the first account of the genus *Nummulites* from the Upper Eocene *Pellatispira*-bearing horizon in the Indian region.

OUTCROPS of marine Upper Eocene rocks with larger foraminifera are known to occur in three areas in the India-Pakistan region (Samanta 1968, fig. 1): Surat-Broach in Western India (Rao 1941), the Sulaiman Range in West Pakistan (Eames 1952) and Assam in Eastern India (Nagappa 1951, Samanta 1965). *Nummulites* has been reported to occur in association with the typical Upper Eocene genus *Pellatispira* in all three areas but so far there is no published account of the genus from this horizon.

In Assam the Kopili Formation contains a rich Upper Eocene larger foraminiferal assemblage including such stratigraphically important genera as *Asterocyclina*, *Discocyclina*, *Nummulites*, and *Pellatispira*. An investigation of the larger foraminifera of the Kopili Formation in the Garo Hills has been carried out by the writer and an account of the genus *Nummulites* is given in the present paper.

KOPILI FORMATION

Evans (1932, pp. 173-5) first called this unit the Kopili alternations 'Stage' and sometimes Kopili 'Stage'. Later workers have changed the name to Kopili Formation, since by original designation it is basically a rock unit. In the type section (Kopili River section of the Kopili-Khorungma region) the succession is reported to be about 450 m. thick and consists of alternations of sandstone, mudstone, shales, carbonaceous rocks, and shell-bearing sandstone. It conformably overlies the Sylhet Limestone and is apparently conformably overlain by the Barail group of rocks. The formation outcrops along the southern fringe of the Shillong Plateau, from the Garo Hills in the west to the Mikir Hills in the east.

In the Garo Hills the Kopili Formation is best exposed in the Simsang River section between Siju Artheke (90° 41' E., 25° 20' N.) and Matmagitik (90° 40' E., 25° 18' N.). It conformably overlies the Siju Limestone and is apparently conformably overlain by Barail-equivalent rocks (Samanta 1968, p. 128, table 1). The lower part of the formation is richly fossiliferous and contains abundant larger foraminifera, including such stratigraphically important genera as *Asterocyclina*, *Discocyclina*, *Nummulites*, and *Pellatispira*. Of these, *Discocyclina* is the most abundant. Because of their much larger size in comparison to other larger foraminifera, discocyclines constitute the most conspicuous element of the foraminiferal fauna. *Nummulites* is represented by small to medium sized striate and reticulate forms and occurs in almost all foraminiferal samples. In contrast

to *Discocyclina* and *Nummulites*, *Asterocyclina* and *Pellatispira* occur in fewer samples and are much less abundant in numbers of individuals.

The following larger foraminifera are identified from the Kopili Formation, Garo Hills (see also Samanta 1968, p. 129, table 2):

<i>Asterocyclina matanzensis</i> Cole	<i>D. sowerbyi</i> Nuttall
<i>Discocyclina archiaci</i> (Schlumberger)	<i>D. sp. cf. D. trabayensis</i> Neumann
<i>D. assamica</i> Samanta	<i>Nummulites chavannesi</i> de la Harpe
<i>D. augustae</i> Weijden	<i>N. sp. aff. N. chavannesi</i> de la Harpe
<i>D. dispansa</i> (Sowerby)	<i>N. fabianii</i> (Prever)
<i>D. eamesi</i> Samanta	<i>N. pengaronensis</i> Verbeek
<i>D. javana</i> (Verbeek)	<i>Pellatispira inflata</i> Umbgrove
<i>D. omphalus</i> (Fritsch)	<i>P. sp. cf. P. irregularis</i> Umbgrove
<i>D. pygmaea</i> Henrici	<i>P. madaraszi</i> (Hantken)
<i>D. sella</i> (d'Archiac)	<i>P. sp. cf. P. orbitoidea</i> (Provale)

Of these, *D. augustae*, *D. sella*, *N. chavannesi*, *N. fabianii*, and *P. madaraszi* are recorded from the Priabonian of North Italy, while *A. matanzensis*, *D. javana*, *D. omphalus*, *D. pygmaea*, *D. sella*, *N. pengaronensis*, and the four species of *Pellatispira* are abundantly represented in the T b of the Indonesian region. The larger foraminiferal assemblage, therefore, indicates a definite Upper Eocene age for the lower part of the Kopili Formation.

Material. The material was collected from five localities in the Garo Hills, previously described (Samanta 1965, p. 416, text-fig. 3). All the four species of *Nummulites* are represented by sufficient material. Presence of free specimens permits a detailed study of these forms. Table 1 shows the distribution of the species in the Garo Hills.

TABLE 1. *Distribution of Nummulites in the Kopili Formation, Garo Hills, Assam*

Species	Localities				
	Sa	Rn	Rgt	N	K
<i>Nummulites chavannesi</i> de la Harpe					X
<i>N. sp. aff. N. chavannesi</i> de la Harpe		X		X	X
<i>N. fabianii</i> (Prever)	X	X			X
<i>N. pengaronensis</i> Verbeek	X	X	X	X	X

Acknowledgements. The author is indebted to Dr. J. R. Haynes for critically reading the manuscript; Dr. F. E. Eames for helpful discussions; Professors H. Hagn and E. Montanaro Gallitelli for comparative material; Drs. F. Bieda and V. Roveda for literature; Professor Alan Wood for providing facilities in his Department; and Mr. H. Williams for help in preparing the plates.

SYSTEMATIC PALAEONTOLOGY

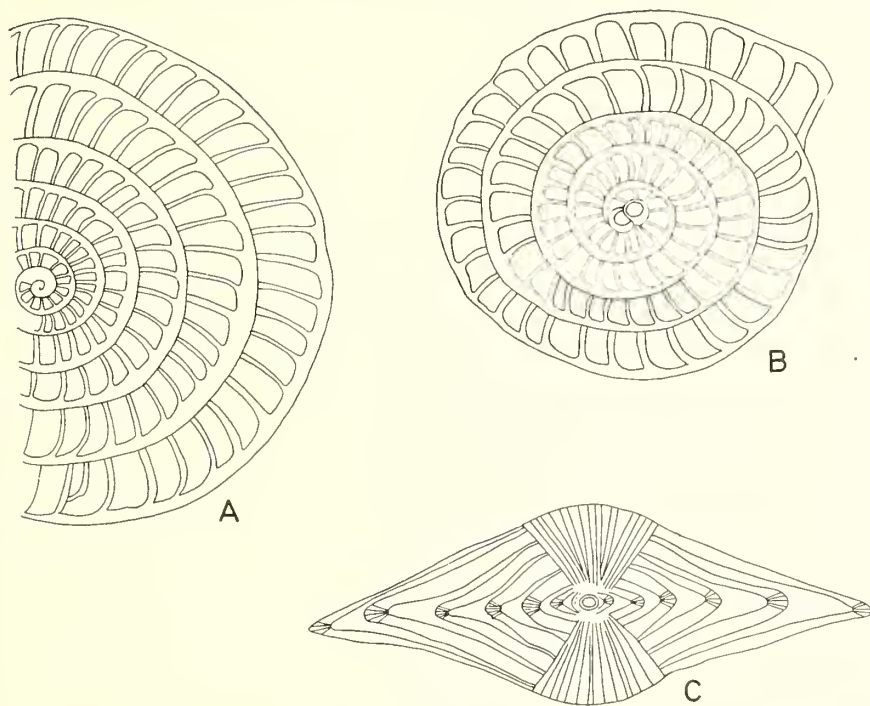
Family NUMMULITIDAE de Blainville 1825
Subfamily NUMMULITINAE de Blainville 1825
Genus NUMMULITES Lamarck 1801

Nummulites chavannesi de la Harpe

Plate 128, figs. 11, 12; Plate 129, figs. 9–14; text-fig. 1

- 1877 *Nummulites chavannesi* de la Harpe, p. 232 (*nom. nud.*).
- 1883a *Nummulites bouillei* var. *ritimeyeri* de la Harpe, pl. 6, figs. 5–11.
- 1883a *Nummulites chavannesi* de la Harpe, pl. 6, figs. 22–41.
- 1883b *Nummulites ritimeyeri* de la Harpe, pp. 162, 163, pl. 30, figs. 9–11.

- 1883b *Nummulites chavannesi* de la Harpe; de la Harpe, pp. 163, 164, pl. 30, figs. 12–18.
 1911b *Nummulites chavannesi* de la Harpe; Boussac, pp. 37, 38.
 1934 *Nummulites* cf. *chavannesi* de la Harpe; Flandrin, pp. 254, 255, pl. 14, figs. 15, 16.
 1934 *Nummulites riitimeyeri* de la Harpe; Flandrin, p. 254, pl. 14, fig. 17.
 1938 *Nummulites riitimeyeri* de la Harpe; Flandrin, pp. 34, 35, pl. 3, figs. 9, 10.
 1951 *Nummulites riitimeyeri* de la Harpe; Daci, pp. 209, 210, pl. 2, figs. 7, 8.
 1951 *Nummulites chavannesi* de la Harpe; Daci, pp. 210, 211, pl. 2, fig. 9.
 1957 *Nummulites chavannesi* de la Harpe; Bieda, pp. 46, 47, pl. 4, figs. 8, 9.
 1960 *Nummulites chavannesi* de la Harpe; Hagn, p. 70, pl. 1, fig. 2; pl. 2, figs. 4, 5.
 1961 *Nummulites chavannesi* de la Harpe; Roveda, pp. 177–81, pl. 14, figs. 1–8.
 1963a *Nummulites chavannesi* de la Harpe; Bieda, pp. 71, 72, 186, pl. 6, figs. 5–7; pl. 7, figs. 1–3.



TEXT-FIG. 1. *Nummulites chavannesi* de la Harpe. A, Part of the equatorial section of a microspheric specimen. $\times 20$ approx. B, Equatorial section of a megalospheric specimen, $\times 25$ approx. C, Axial section of a megalospheric specimen, $\times 25$ approx. All from locality K.

Material. Megalospheric form—25 specimens examined externally, 5 specimens studied in equatorial section, and 5 in axial section. Microspheric form—6 specimens examined externally, 3 specimens studied in equatorial section, and 2 in axial section.

Description. *Megalospheric form.* Test small, lenticular, with slightly elevated polar region surrounded by sloping peripheral part; margin acute. Surface ornamented with well-developed polar pustules from which thin, straight to gently curved septal filaments radiate. Diameter of test varies from 1.9 to 3.4 mm., thickness from 0.9 to 1.4 mm., ratio of diameter to thickness from 2.2 to 2.7, and diameter of polar pustules from 0.4 to 0.6 mm.

About $4\frac{1}{2}$ to 6 regularly coiled whorls open rapidly. Spiral lamina thin and in outer

whorls height of spiral cavity about 4 to 6 times thickness of spiral lamina. Septa nearly perpendicular to spiral lamina, straight with sharp curvature near distal end. About 8–11 septa occur in 1st whorl; 15–20 in 2nd; 19–28 in 3rd; 24–9 in 4th; and 28–32 in 5th.

Small, subcircular first chamber followed by subequal, reniform second chamber. Separating wall either straight or curved outwards. Diameters of first chamber vary from 0.055×0.050 mm. to 0.095×0.075 mm. and those of second chamber from 0.055×0.045 mm. to 0.100×0.060 mm. Distance across both chambers varies from 0.105 to 0.180 mm. Equatorial chambers quadrate in shape and about twice as high as long.

In axial section first chamber circular and about 0.05 mm. in height. Chamber cavity triangular in shape. Alar prolongations wide open. Marginal cord distinct. Wedge-shaped polar plugs always very conspicuous and about 0.6 mm. in diameter near surface.

Microspheric form. Test small with well-developed, slightly elevated polar pustules; margin acute. Septal filaments thin, radiate, nearly straight. Diameter of test varies from 3.8 to 5.0 mm., thickness from 1.8 to 2.0 mm., ratio of diameter to thickness from 2.1 to 2.4 mm., and diameter of polar pustules from 0.8 to 1.0 mm.

There are about 9 whorls in diameter of 4.2 mm. Whorls regularly coiled and open rather rapidly. In outer whorls height of spiral cavity about 3 times thickness of spiral lamina. Septa nearly perpendicular and straight with sharp curvature at top. Chambers quadrate, about 2 to 3 times higher than long.

In axial sections alar prolongations wide open. Marginal cord distinct. Well-developed polar plugs wedge-shaped, about 1.0 mm. in diameter near surface.

Remarks. The presence of well-defined polar pustules, high equatorial chambers between almost straight septa, and wide alar prolongations distinguish this species from the associated nummulites in the Kopili Formation. The Assam specimens have been compared with European material, provided by Professor H. Hagn. They are closely similar to the Priabonian material described and illustrated by Roveda (1961).

Distribution. *N. chavannesesi* has been reported from Italy, Spain, France, Switzerland, Poland, Hungary, Albania, Turkey, Algeria, Egypt, and Somaliland. Its known range is from Upper Eocene to Oligocene.

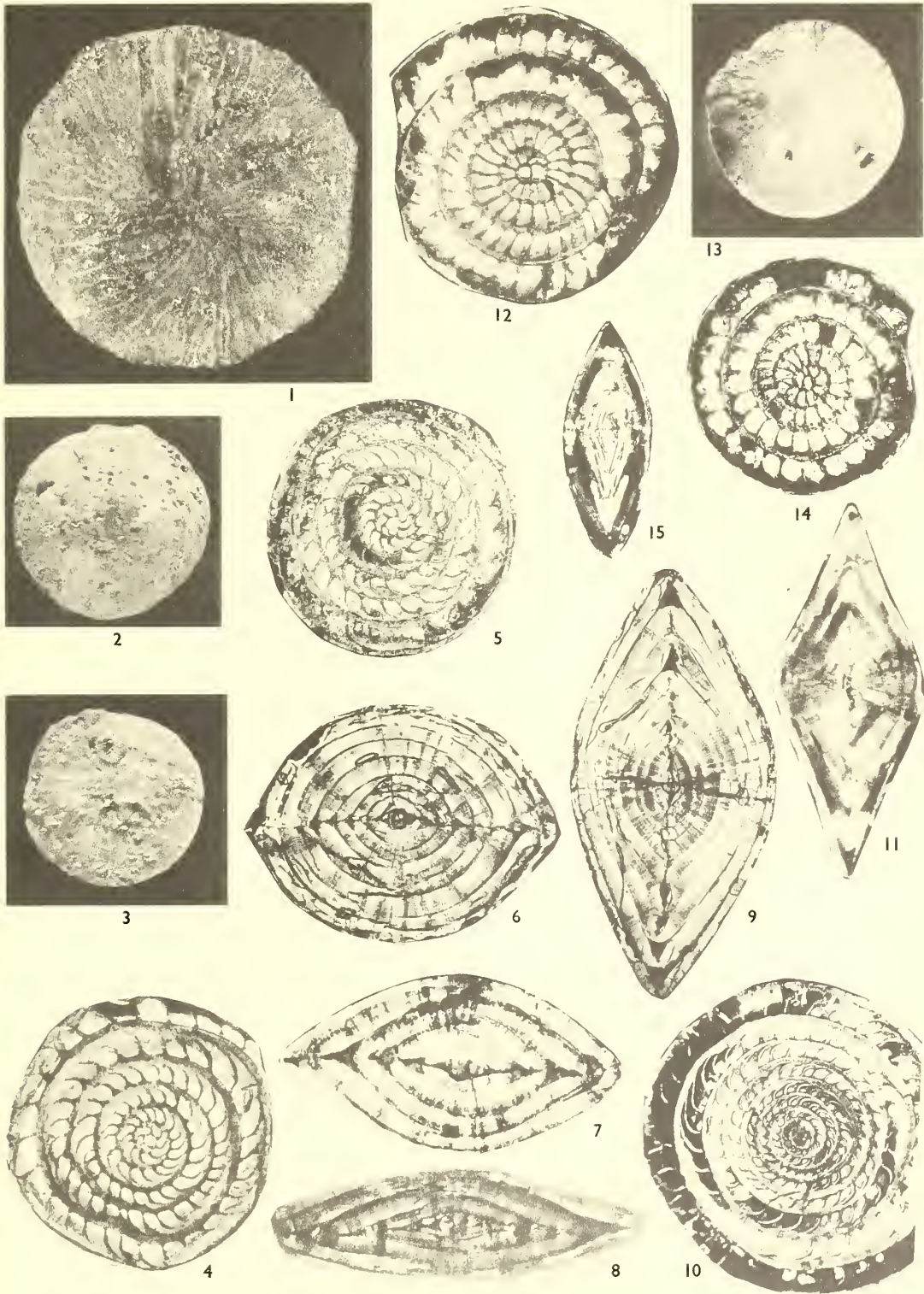
In the Garo Hills *N. chavannesesi* occurs only in the Upper Eocene Kopili Formation (Table 1). There is no report of its occurrence in the other Upper Eocene localities in India and adjacent countries. The present record of *N. chavannesesi* extends its geographic distribution considerably.

EXPLANATION OF PLATE 128

Figs. 1–10. *Nummulites pengaronensis* Verbeek. 1, External view of microspheric specimen, $\times 6$. 2, 3, External views of megalospheric specimens; 2, inflated variety, $\times 6$; 3, compressed lenticular variety, $\times 9$. 4, 5, Equatorial sections of megalospheric specimens, $\times 15$; 4, inflated variety; 5, lenticular variety. 6–8, Axial sections of megalospheric specimens showing variation in transverse views of tests; 6, $\times 15$; 7, 8, $\times 21$. 9, Axial section of microspheric specimen, $\times 9$. 10, Equatorial section of microspheric specimen, $\times 9$. 1, 3, 8, 10, from locality Sa; 2, 7, from locality K; 4, 5, from locality Rn; 6, 9, from locality N (see Samanta 1965, p. 416).

Figs. 11, 12. *Nummulites chavannesesi* de la Harpe. 11, Axial section of megalospheric specimen, $\times 21$. 12, Equatorial section of megalospheric specimen, $\times 21$. Both from locality K.

Figs. 13–15. *Nummulites* sp. aff. *N. chavannesesi* de la Harpe. 13, External view of megalospheric specimen, $\times 15$. 14, Equatorial section of megalospheric specimen, $\times 21$. 15, Axial section of megalospheric specimen, $\times 21$. All from locality K.



SAMANTA, Upper Eocene *Nummulites*

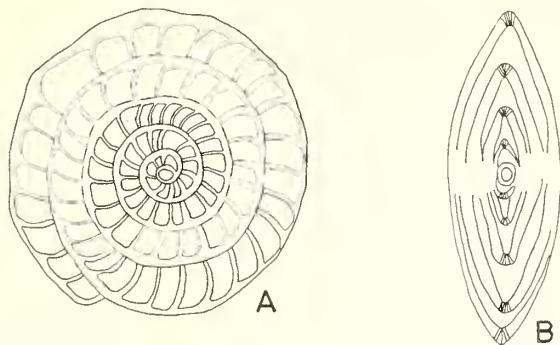
Nummulites sp. aff. *N. chavannesi* de la Harpe

Plate 128, figs. 13–15; text-fig. 2

Material. Only megalospheric specimens were observed. 15 specimens examined externally, 5 specimens studied in equatorial section, and 2 in axial section.

Description. *Megalospheric form.* Test very small, lenticular, with acute margin. Septal filaments thin and radial. Diameter of test varies from 1.6 to 2.0 mm., thickness from 0.56 to 0.80 mm., and ratio of diameter to thickness from 2.0 to 3.4.

Spire is regular with about $4\frac{1}{2}$ to $5\frac{1}{2}$ whorls increasing regularly in height. Spiral lamina thin, about $\frac{1}{5}$ height of spiral cavity in thickness. Septa are perpendicular to wall and



TEXT-FIG. 2. *Nummulites* sp. aff. *N. chavannesi* de la Harpe (megalospheric form.) A, Equatorial section. B, Axial section. Both from locality K, $\times 25$ approx.

nearly straight with curvature at top. About 8–10 septa occur in 1st whorl; 15–18 in 2nd; 19–25 in 3rd; 24–6 in 4th; and 24–30 in 5th.

Subcircular first chamber followed by subequal, crescentic second chamber. Separating wall gently curved outwards. Diameters of first chamber vary from 0.05×0.03 mm. to 0.08×0.07 mm.; those of second chamber from 0.055×0.035 mm. to 0.10×0.055 mm. Distance across both chambers varies from 0.09 to 0.15 mm. Equatorial chambers quadrate and higher than long.

In axial section first chamber circular, about 0.06 mm. in height. Alar prolongations wide open. Marginal cord distinct.

Remarks. The present specimens are closely similar to *N. chavannesi* in internal characters, but can easily be distinguished from the latter by the shape of the test and the absence of polar pustules. They are provisionally identified as *N. sp. aff. N. chavannesi*.

Distribution. The species occur in localities Rn, N, and K in the Garo Hills (Samanta 1965, p. 416). The presence of similar forms has also been noticed by the writer in the Upper Eocene of Surat-Broach, Western India.

Nummulites fabianii (Prever)

Plate 129, figs. 1–8; text-fig. 3, 4

1905 *Bruguieria fabianii* Prever in litt.; Fabiani, pp. 1805, 1811, 1824.

1905 *Bruguieria sub-fabianii* Prever in litt.; Fabiani, pp. 1811, 1824.

- 1906 *Nunnuulites fabianii* (Prever in Fabiani); Boussac, pp. 88–90, pl. 1, figs. 1–5, 7–9; pl. 3, fig. 6.
- 1911a *Nunnuulites fabianii* Prever in Fabiani; Boussac, pp. 40, 72, pl. 10, figs. 1, 2, 28; pl. 17, figs. 8, 11, 13.
- 1911b *Nunnuulites fabianii* Prever in Fabiani; Boussac, pp. 79–84, pl. 1, figs. 6, 13; pl. 4, figs. 9, 10.
- 1928 *Nunnuulites fabianii* Prever; de Cizancourt, p. 294, pl. 2, fig. 10.
- 1930 *Nunnuulites fabianii* Prever; de Cizancourt, pp. 209, 210, pl. 22, figs. 4, 7; pl. 23, fig. 5.
- 1934 *Nunnuulites fabianii* Prever; Flandrin, p. 259, pl. 1, fig. 20.
- 1951 *Nunnuulites fabianii* Prever; Daci, pp. 221, 222, pl. 3, figs. 1, 2.
- 1951 *Nunnuulites subfabianii* Prever; Daci, pp. 222–4, pl. 3, figs. 4–7.
- 1957 *Nunnuulites fabianii* Prever; Bieda, p. 30, pl. 5, fig. 5.
- 1959 *Nunnuulites retiatius* Roveda, pp. 201–7, pl. 1, figs. 1–11.
- 1960 *Nunnuulites fabianii* (Prever); Hagn, p. 149, pl. 2, figs. 2, 3, 7.
- 1961 *Nunnuulites fabianii* (Prever); Roveda, pp. 161–9, pl. 15, figs. 15, 16; pl. 17, figs. 8, 9; pl. 18, figs. 4, 5; pl. 19, figs. 1, 6–8, 14–16.
- 1963a *Nunnuulites fabianii* Prever; Bieda, pp. 101–4, 195, 196, pl. 15, fig. 9; pl. 16, figs. 1–4.
- 1963b *Nunnuulites fabianii* Prever; Bieda, pp. 201–4, 214–15, pl. 13, figs. 3, 4.
- 1965 *Nunnuulites fabianii* Prever; Bozorgnia and Kalantari, pp. 17, 18; pl. 20, figs. 1–7.

Material. Megalospheric form—20 specimens examined externally, 5 studied in equatorial section, and 7 in axial section. Microspheric form—10 specimens examined externally, 4 studied in equatorial section, and 1 in axial section.

Description. *Megalospheric form.* Test small, lenticular, with subacute margin. Surface ornamented with spirally arranged rectangular meshes produced by intersections of radial filaments with raised spiral line. Spirally arranged granules joined together by 'transverse lamina' produce raised spiral line. In some specimens granules cluster at poles to form polar pustules. Diameter of test varies from 1.8 to 3.0 mm., thickness from 1.25 to 1.85 mm., and ratio of diameter to thickness from 1.4 to 1.9.

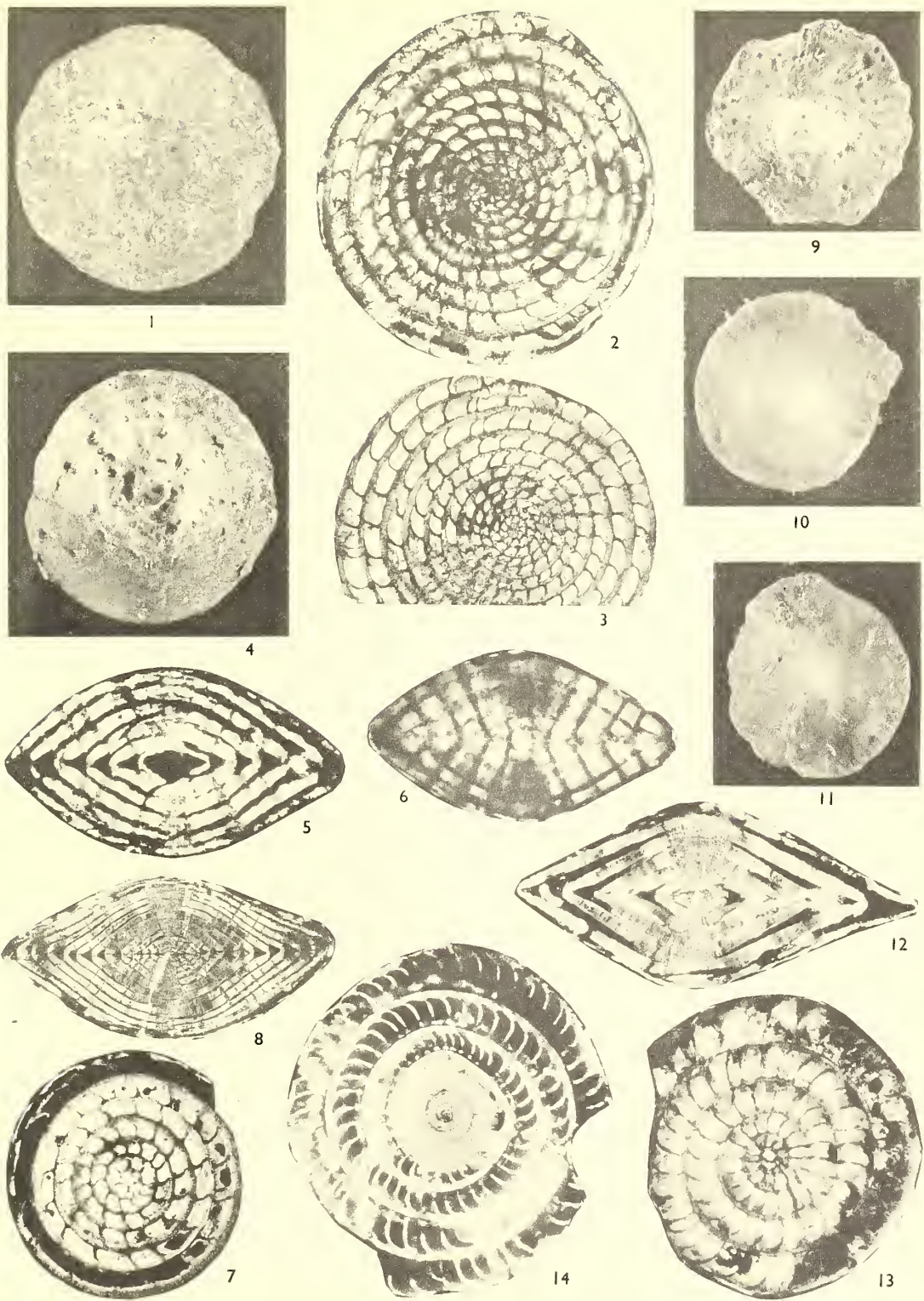
About 5 to $6\frac{1}{2}$ regularly coiled whorls occur, increasing slowly in height. Spiral lamina thick, and in some inner whorls may be as thick as height of spiral cavity. Near periphery height of spiral cavity about 2 to 3 times thickness of spiral lamina. Septa slightly inclined to spiral wall, straight to gently curved in their course. About 6–7 septa occur in 1st whorl; 9–13 in 2nd; 12–16 in 3rd; 15–20 in 4th; and 16–22 in 5th.

Subcircular first chamber followed by smaller, semicircular to reniform second chamber. Separating wall either straight or curved outwards. Diameters of first chamber vary from 0.130×0.095 mm. to 0.20×0.20 mm.; those of second chamber from 0.10×0.05 mm. to 0.175×0.095 mm. Distance across both chambers varies from 0.16 to 0.28 mm. Chambers quadrate in shape. Near centre, chambers almost as long as high, but in ontogeny chambers become considerably longer, so that in outer whorls chambers become twice as long as high.

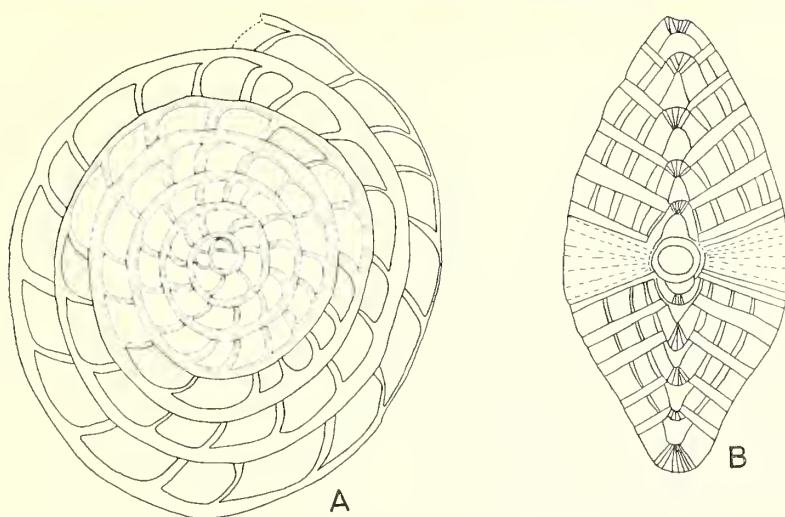
EXPLANATION OF PLATE 129

Figs. 1–8. *Nunnuulites fabianii* (Prever). 1, External view of microspheric specimen, $\times 6$. 2, 3, Equatorial sections of microspheric specimens, $\times 9$. 4, External view of megalospheric specimen, $\times 15$. 5, 6, Axial sections of megalospheric specimens, $\times 21$. 7, Equatorial section of megalospheric specimen, $\times 15$. 8, Axial section of microspheric specimen, $\times 7.5$. All from locality Rn (see Samanta 1965, p. 416).

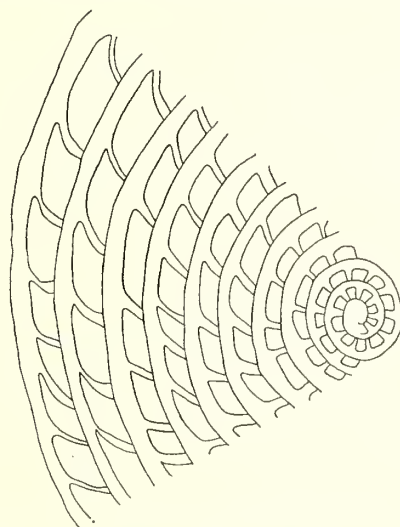
Figs. 9–14. *Nunnuulites chavaunesi* de la Harpe. 9, External view of microspheric specimen, $\times 6$. 10, 11, External views of megalospheric specimens, $\times 12$. 12, Axial section of megalospheric specimen, $\times 21$. 13, Equatorial section of megalospheric specimen, $\times 21$. 14, Equatorial section of microspheric specimen, $\times 15$. All from locality K.



SAMANTA, Upper Eocene *Nummulites*



TEXT-FIG. 3. *Nummulites fabianii* (Prever) (megalospheric form). A, Equatorial section. B, Axial section. Both from locality Rn, $\times 25$ approx.



TEXT-FIG. 4. *Nummulites fabianii* (Prever). Part of the equatorial section of a microspheric specimen from locality Rn, $\times 18$ approx.

In axial section first chamber circular, about 0.10 to 0.13 mm. in height. Spiral lamina rather thick. There may be reduction in thickness of spiral lamina at periphery. Alar prolongations narrow to moderately open. Marginal cord distinct. Pillars well-developed, start from marginal cord of each whorl, and of uniform thickness throughout length. At poles, pillars cluster together to form polar plugs. Diameter of pillars varies from 0.050 to 0.075 mm. and polar plugs from 0.25 to 0.50 mm.

Microspheric form. Test medium-sized, lenticular, with subacute margin. Surface of

test ornamented with thin, reticulate septal filaments. In young individuals rectangular meshes are discernible but in adult specimens branching filaments produce complex network. Diameter of test varies from 5.1 to 8.4 mm., thickness from 2.7 to 4.2 mm., and ratio of diameter to thickness from 1.9 to 2.2.

In equatorial section about 9 to 13 whorls occur, coiled regularly and increasing slowly in height during ontogeny. Spiral lamina rather thick. In adult whorls height of spiral cavity usually greater than thickness of spiral lamina. Septa inclined to whorl wall, and straight to gently curved in their course. Equatorial chambers longer than high, and in outer whorls 3 to 4 times as long as high.

In axial section, alar prolongations narrow to moderately open. Marginal cord distinct. Pillars moderately developed. Each pillar starts from marginal cord and extends up to surface. Diameter of pillars varies from 0.05 to 0.15 mm. In polar region pillars cluster together to form polar plug-like structures about 0.8 mm. in diameter near surface.

Remarks. Both in external and internal features the present form is distinctive. The reticulate ornamentation, the long equatorial chambers, and the pillared axial section enables the species to be distinguished from the associated nummulites in the Kopili Formation. The Assam specimens were compared with those of *N. fabianii* from North Italy provided by Professor Montanaro-Gallitelli.

Because of their distinctive morphological features and wide geographic distribution in the rocks of Upper Eocene to Oligocene age, the reticulate *Nummulites* have received particular attention and several species have been described. But at present there is considerable difference of opinion about the validity of a number of these forms (see Eames *et al.* 1959; Bieda 1963*b*); consequently, application of reticulate *Nummulites* species in the finer biostratigraphic zonation of Upper Eocene–Oligocene rocks is lacking.

Distribution. *N. fabianii* is one of the most widely distributed representatives of the genus, reported from the Upper Eocene of Italy, Spain, France, Switzerland, Poland, Hungary, Albania, Rhodes Island, Turkey, Morocco, Algeria, Tunisia, Libya, Egypt, and Iran.

In the Garo Hills *N. fabianii* occurs in the Kopili Formation at localities Sa, Rn, and K (Table 1). It occurs also in two other Upper Eocene localities in the Indian region; in the Sulaiman Range its presence has been noted by Bayliss (1961), while the writer has observed it in Surat-Broach in association with *Pellatispira* spp., etc.

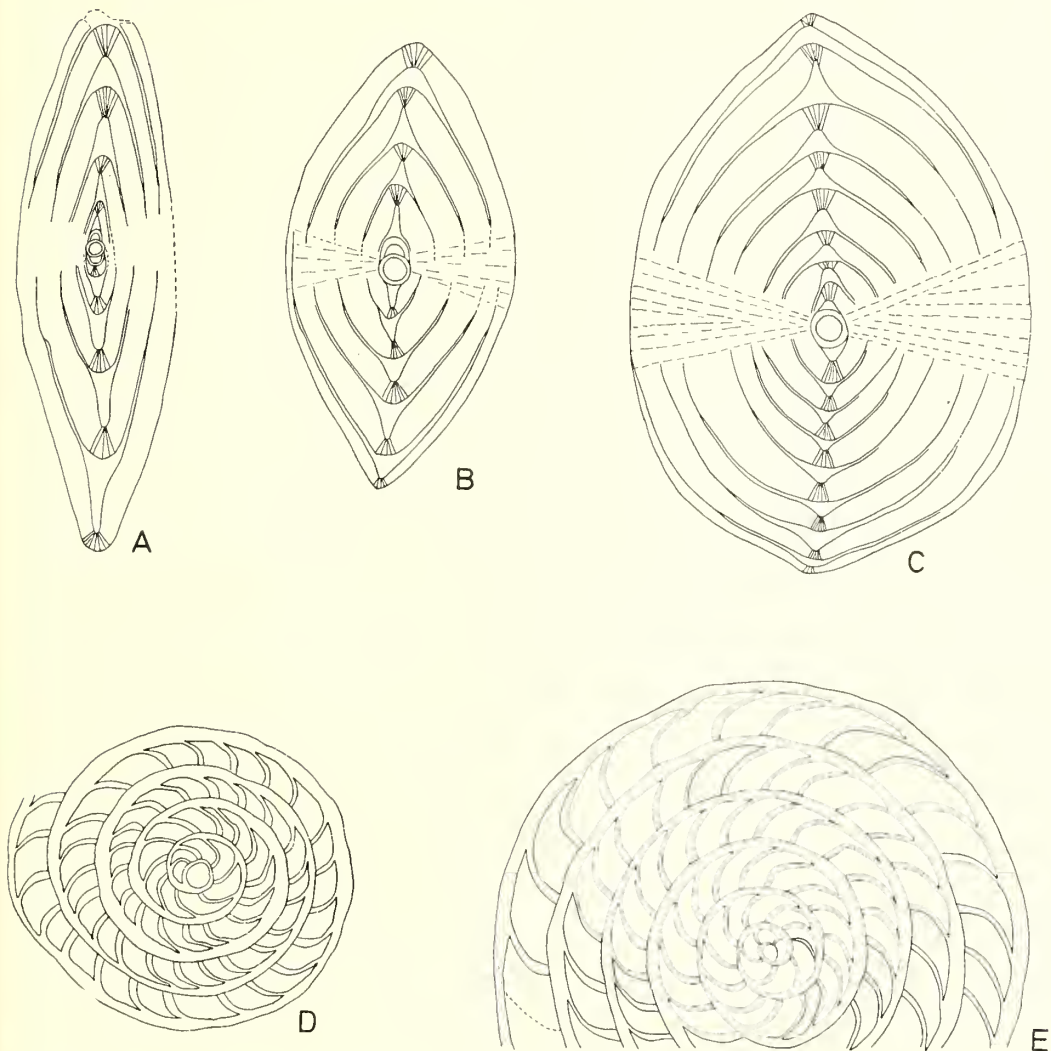
There is no authentic record of reticulate *Nummulites* from the Upper Eocene of the Malayan Archipelago (Cole 1963, Adams 1965). The only report of an occurrence in association with a typical Upper Eocene assemblage from this region was that by Cole (Cloud and Cole 1953, p. 323) who later (1963, pp. E4, E14) postulated that the Upper Eocene species in the assemblage are reworked specimens and that reticulate *Nummulites* do not occur in the Eocene of the Malayan Archipelago. Thus, Assam is the easternmost locality with *N. fabianii*.

Nummulites pengaronensis Verbeek

Plate 128, figs. 1–10; text-figs. 5, 6

- 1871 *Nummulites pengaronensis* Verbeek, pp. 3–6, pl. 1, figs. 1a–k.
- 1892 *Nummulites nanggoelani* Verbeek, pp. 116, 118.
- 1896 *Nummulites nanggoelani* Verbeek; Verbeek and Fennema, p. 1152, pl. 8, figs. 111–13.
- 1896 *Nummulites pengaronensis* Verbeek; Verbeek and Fennema, pp. 1153, 1154.
- 1912 *Nummulites pengaronensis* Verbeek; Douvillé, pp. 284, 285, pl. 24, fig. 6.

- 1921 *Nummulites* cf. *pengaronensis* Verbeek; Yabe, pp. 104, 105, pl. 18, fig. 8.
 1929 *Nummulites pengaronensis* Verbeek; Vlerk, pp. 20, 21, figs. 12, 35a, b.
 1932 *Camerina pengaronensis* (Verbeek); Doornink, pp. 283, 284, pl. 4, figs. 1-3; pl. 6, fig. 12.
 1934 *Camerina pengaronensis* (Verbeek); Henrici, pp. 29, 30, pl. 1, fig. 10.
 1934 *Camerina* cf. *pengaronensis* (Verbeek); Caudri, p. 52.
 1953 *Camerina saipanensis* Cole, pp. 20, 21, pl. 2, figs. 7-19.
 1957 *Camerina pengaronensis* (Verbeek); Cole, pp. 753, 754, pl. 231, figs. 1-17.
 1959a *Nummulites pengaronensis* Verbeek; Nagappa, pp. 163, 166, pl. 10, figs. 3-5.
 1965 *Nummulites* cf. *saipanensis* (Cole); Adams, p. 313, pl. 23, fig. c.

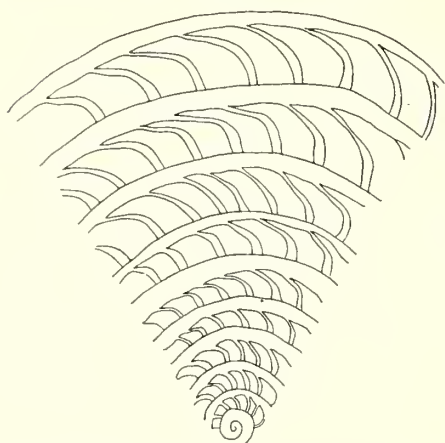


TEXT-FIG. 5. *Nummulites pengaronensis* Verbeek (megalospheric form). A-C, Axial sections, $\times 25$ approx.; A, from locality Sa; B, from locality K; C, from locality N. D, Split specimen from locality Sa, $\times 20$ approx. E, Equatorial section from locality Rn, $\times 25$ approx.

Material. Megalospheric form—75 specimens examined externally, 5 studied in equatorial section, and 12 in axial section. Microspheric form—12 specimens examined externally, 3 studied in equatorial section, and 4 in axial section. In addition, 23 split specimens of megalospheric form and 3 of microspheric form were studied in equatorial view.

Description. Megalospheric form. Test small, compressed, lenticular to globose, with acute margin. Surface marked by thin, radial septal filaments, straight to gently curved at ends. Diameter of test varies from 2.0 to 5.2 mm., thickness from 0.8 to 3.3 mm., and ratio of diameter to thickness from 1.3 to 3.6.

Spire more or less regular with about 5 to 7 whorls increasing regularly in height, with exception of last whorl, which may be narrower than preceding one. Height of spiral cavity in outer whorls about 3 times thickness of spiral lamina. Septa nearly perpendicular to inclined at their base, straight for about half their course, then curve sharply backwards. Thickness of septa decreases considerably from proximal to distal end. About 6–7 septa occur in 1st whorl; 11–14 in 2nd; 17–19 in 3rd; 23–6 in 4th; 24–7 in 5th; 26–9 in 6th; and 29–32 in 7th.



TEXT-FIG. 6. *Nummulites pengaronensis* Verbeek. Part of the equatorial section of a microspheric specimen from locality Sa, $\times 18$ approx.

First chamber circular to elliptical in equatorial section, followed by usually smaller, crescentic to reniform second chamber. Separating wall curved outwards. Diameters of first chamber vary from 0.125×0.120 mm. to 0.275×0.225 mm., those of second chamber from 0.105×0.050 mm. to 0.175×0.075 mm. Distance across both chambers varies from 0.200 to 0.325 mm. Equatorial chambers subquadrate to falciform in shape, usually higher than long, although reverse also quite common.

In axial section first chamber circular, about 0.100 to 0.175 mm. in height. Alar prolongations extremely narrow. Appreciable reduction in thickness of spiral lamina at periphery. Marginal cord distinct. Traces of weakly developed pillar-like structures in polar region.

Microspheric form. Test small- to medium-sized, lenticular, with acute margin. Septal filaments radial, straight. Diameter of test varies from 4.6 to 8.9 mm., thickness from 1.9 to 3.3 mm., and ratio of diameter to thickness from 2.0 to 3.3.

In equatorial section about 9 to 13 whorls occur, regularly increasing in height. Height of spiral cavity greater than thickness of spiral lamina. Septa nearly perpendicular at base, straight for about half their course, then curve sharply backwards. Thickness of septa decreases considerably from proximal to distal end. Chambers subquadrate to falciform, usually higher than long.

In axial section chamber cavity triangular in shape. Alar prolongations extremely narrow. Considerable reduction in thickness of spiral lamina at periphery. Marginal cord weakly developed. In polar region traces of pillar-like structures.

Remarks. Although the Assam specimens show considerable variation in external form

of the test, they are identical in internal structures and are included here under one species. They are characterized externally by the presence of radial septal filaments and the absence of distinct polar pustules, and internally by the characters of the septa in equatorial section and very narrow alar prolongations in axial section.

Nummulites saipanensis (Cole), originally described from Saipan, Mariana Islands (Cole and Bridge 1953), was later considered by its author (Cole 1957) to be synonymous with *N. pengaronensis* Verbeek. This is accepted here. Cole (op. cit.) also included *Nummulites semiglobula* (Doornink), described from Java (Doornink 1932), in the synonymy of *N. pengaronensis*. However, although *N. semiglobula*, as well as *N. gerthi*, bear some resemblance to *N. pengaronensis*, a more detailed study based on the topotype material of these two species is needed before considering them as junior synonyms of *N. pengaronensis*.

Among the European species, *Nummulites stellatus* Roveda described from the Priabonian of North Italy (Roveda 1961), is very closely similar to *N. pengaronensis* in internal morphology.

Sen Gupta (1965), while working on some Middle Eocene *Nummulites* from Western India, regarded *N. pengaronensis* as a junior synonym of *Nummulites beaumonti* d'Archiac and Haime. Under the remarks on *N. beaumonti*, Sen Gupta (op. cit., p. 93) wrote: 'Another synonym of *N. beaumonti* is *N. pengaronensis* Verbeek, a wide-spread Indo-Pacific form. It shows a tight coiling of spiral wall, which is almost uniformly thick, and small embryonic chambers, as does typical *N. beaumonti*. These features are clearly seen in the figures of *N. pengaronensis* published by Cole (1957a, pl. 231, figs. 1-17) and have been confirmed by an examination of Cole's material from Eniwetok.' Sen Gupta, therefore, neither examined the type or topotype materials nor consulted the type description and illustrations of *N. pengaronensis* to support his remarks. Further, he did not compare his Indian specimens of *N. beaumonti* with ones from the Indian region identified as *N. pengaronensis* by other workers. (There are good illustrations of microspheric and megalospheric specimens of *N. pengaronensis* from Eastern India (Nagappa 1959a, b). In both these publications, there are good illustrations of *N. beaumonti* too, and in the latter Nagappa has pointed out (p. 158, pl. 21, figs. 1, 2) the conspicuous difference in the character of the septa in these two species.) A thorough comparison between the two species, including such taxonomically important features as the characters of the equatorial chambers and the septa as seen in equatorial section, has not been made and Sen Gupta's remarks do not appear to be justified.

A comparison of the description and illustrations of *N. beaumonti* provided by Davies (1940) with those of *N. pengaronensis* given by Verbeek (1871), Doornink (1932), and others, shows clearly that they are two distinct species. In equatorial section they can always be separated by the characters of the septa and the equatorial chambers, and in axial section by the width of the alar prolongations and the degree of development of polar plugs. The writer believes that these two species are not only distinct but that they belong to two different groups of species. If *N. pengaronensis* is considered to be a synonym of *N. beaumonti*, or in other words, if the morphological differences between them are not considered to be of specific importance, then the usefulness of species of *Nummulites* in the stratigraphic analysis and correlation of the Lower Tertiary will be greatly reduced. With *N. pengaronensis* as a junior synonym, the stratigraphic range of *N. beaumonti* would be from Middle Eocene to Oligocene (not Middle to Upper

Eocene as mentioned by Sen Gupta (1965, p. 92)) and it would then be difficult to use it as a 'key' species in stratigraphy.

Distribution. *N. pengaronensis* is a widely distributed Indo-Pacific form and has been reported from the Central Pacific Islands, the East Indies, Burma, Eastern India, and Western Pakistan. Its known stratigraphic range is from the upper part of the Middle Eocene to Oligocene.

In the Garo Hills *N. pengaronensis* ranges from the Upper Member of the Siju Limestone (Middle Eocene) to the overlying Kopili Formation (Upper Eocene). It is the most abundant representative of the genus in the Kopili Formation and occurs in all the five localities (see Table 1).

Although it is known to occur in the Sulaiman Range (Eames 1952), there is no report of the species from the Upper Eocene of Surat-Broach, Western India.

GENERAL REMARKS

The four species of *Nummulites* recorded from the Kopili Formation belong to three different groups. *N. fabianii* (Prever) belongs to the reticulate group of forms characteristic of Upper Eocene to Oligocene. This is the only pillared form in the present assemblage. Of the three remaining striate forms, *N. pengaronensis* with its strongly curved septa and very narrow alar prolongations is distinctly different from *N. chavannesi* and *N. sp. aff. N. chavannesi*, characterized by rapid opening of the whorls, straight septa, and wider alar prolongations. In all these four forms the marginal cord is only moderately developed and the size of the tests does not exceed 9 mm. The striate forms are much more abundant than the reticulate one, and occur in almost all foraminiferal samples.

The assemblage of *Nummulites* in the Kopili Formation is markedly different from that in the underlying Upper Member of the Siju Limestone (Samanta 1968). In the latter horizon the assemblage is characterized by the presence of large, highly evolved species showing three 'parts' in the spire as recognized by Schaub (1963). These forms are totally absent in the Kopili Formation. Also, the number of species of *Nummulites* is fewer in the Kopili Formation than in the underlying Siju Limestone. Throughout the range of the genus in the Indian region the most striking change in the assemblages occurs at this horizon. The total absence of the typical representatives of the genus characterizing the older horizons, together with the appearance of a new group of forms in the Kopili Formation, makes the assemblage more akin to that of the Oligocene than to that of underlying Middle Eocene horizon. Indeed, in the absence of reticulate species it is difficult to distinguish the *Nummulites* assemblage of the Upper Eocene from that of the Oligocene.

In the presence of *N. fabianii* and abundant small to medium striate forms, the present assemblage is closely comparable to that recorded in the Priabonian of Europe. It is distinguished from the latter essentially by the absence of the *Nummulites striatus-garnieri* group of forms, which are common in the European Upper Eocene. The *Nummulites* assemblage in the Kopili Formation is, however, quite distinct from that known from the Upper Eocene of the Far East. *N. pengaronensis* is the only species common to the two regions. The *Nummulites yawensis-djokdjokartae* group of forms described from the Upper Eocene of the Malayan Archipelago are absent in the Kopili Formation of Assam. The absence of the well-known and widely distributed Upper Eocene reticulate *Nummulites* in the Far East constitutes the most striking difference between the Upper Eocene *Nummulites* assemblages of the two regions.

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BIMAL K. SAMANTA
Department of Geology
University College of Wales
Aberystwyth, Wales

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A NEW PLANT FROM THE LOWER OLD RED SANDSTONE OF SOUTH WALES

by DIANNE EDWARDS

ABSTRACT. A new plant is described from the Senni Beds of the Lower Devonian of South Wales. The naked axes were pseudomonopodially and dichotomously branched and contained protosteles in which the protoxylem was central. Terminal fructifications consisted of sporangia alternating with sterile bracts; the plant was homosporous. A comparison is made with other Devonian genera, which show similar organization in the fertile regions, and it is concluded that the plant should be placed in a new genus, *Krithodeophyton*, assigned to the Barinophytaceae (Incertae sedis).

THE fossils described in this paper were among those collected by Croft from the Brecon Beacons Quarry, also called the Storey Arms Quarry (Nat. Grid Ref. SO 972208) and are now in the Department of Palaeontology, British Museum (Natural History). The quarry is in the Senni Beds, which form the lower part of the Breconian Stage of the Lower Old Red Sandstone in South Wales (Croft 1953) and are probably equivalent to the Siegenian of Europe. Among the plants previously described from this locality are *Gosslingia breconensis*, *Zosterophyllum llanoveranum*, and *Drepanophycus spinaeformis* (Heard 1927 and 1939, Croft and Lang 1942, Edwards and Banks 1965, Edwards 1967). The majority of the plants were preserved as compressions in a fine-grained, blue-grey sandstone, but parts of the axes were sometimes petrified.

Small pieces of cuticle were recovered after bulk maceration of the rock in commercial strength (40%) hydrofluoric acid. These were then treated with Schulze's solution (concentrated nitric acid and potassium chlorate) for 1–8 hours and, when the carbon had oxidized and the outlines of cells were visible, the fragments were washed, immersed in Diaphane solvent and mounted in Diaphane (Distributors: Will Scientific Inc., New York 52, N.Y., U.S.A.). Pieces of carbon were also picked off both axes and sporangia with steel needles, macerated in Schulze's solution and mounted in the same way. Film pulls were made from those fossils, which were exposed on the surface of the rock. A solution of cellulose nitrate in amyl acetate was poured over the fossil and left to dry overnight. The resulting rough, transparent film was peeled off and mounted in Harleco Synthetic Resin (H.S.R.). (Distributors: Arthur H. Thomas Company, Philadelphia, Pa., U.S.A.).

The anatomy of the pyritised axes was investigated using a modification of the method described by Beck in 1955. A small piece of rock containing a petrified fossil was first embedded in the synthetic resin, Ceemar, because the rock matrix tended to crumble when sawn (Leclercq and Noel 1953). The transparent block of plastic was trimmed to size and cut into sections about a millimetre thick. These were ground smooth on a glass plate with grade 600 carborundum powder, washed and then treated in chromic oxide powder until a good polish was obtained. After washing they were dried, soaked in xylol and mounted in H.S.R. The sections of the axes were then examined using a Leitz Ultropak microscope. All the preparations have been deposited in the Department of Palaeontology, British Museum (V26578, V26579, V52137–54).

SYSTEMATIC DESCRIPTION

Family BARINOPHYTACEAE Kräusel and Weyland 1961

Genus KRITHODEOPHYTON gen. nov.

Type species. Krithodeophyton croftii sp. nov.

Diagnosis. Plant consisting of naked, pseudomonopodially branching axes with some dichotomous branching in distal parts. Simple protostele composed of mainly scalariform, but some reticulate tracheids; protoxylem central. Sporangia in terminal spikes. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia borne in two rows, one on either side of the axis. Narrow sterile appendages, attached at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells. Plant homosporous. Spores assignable to the dispersed spore genus *Apiculiretusispora* (*sensu* Streel 1964).

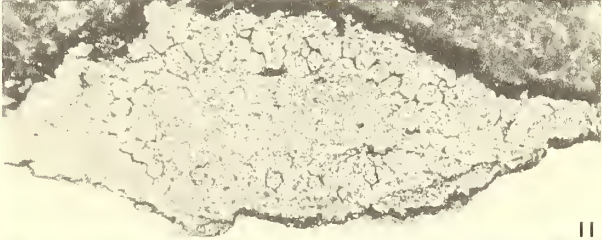
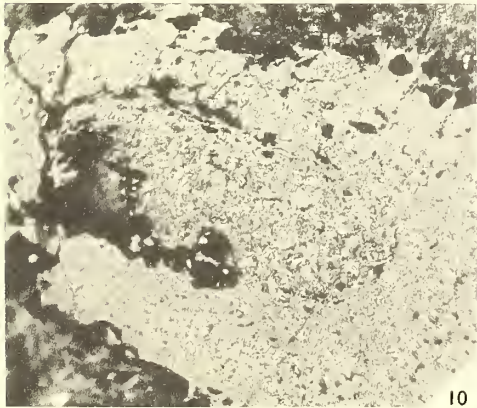
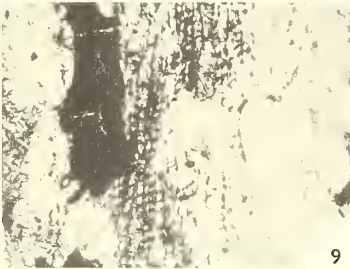
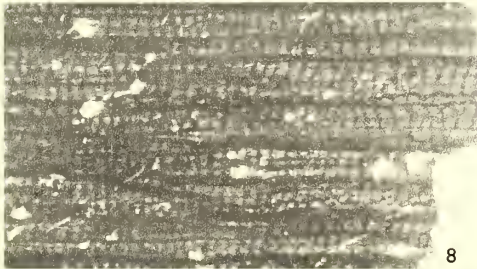
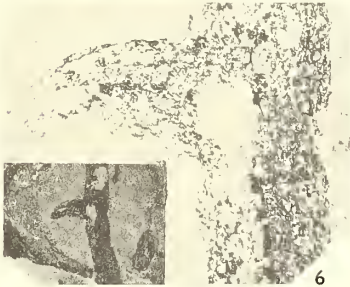
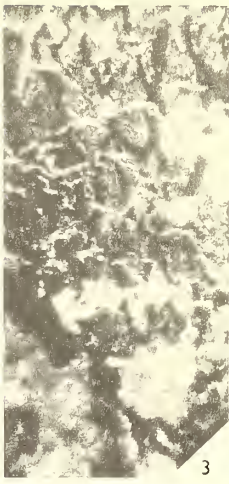
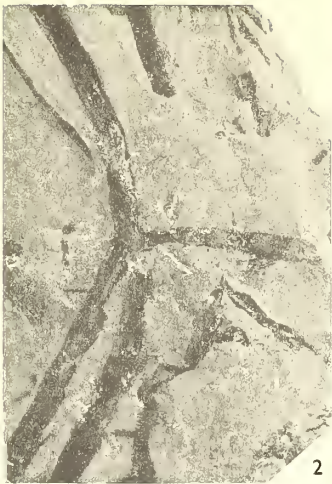
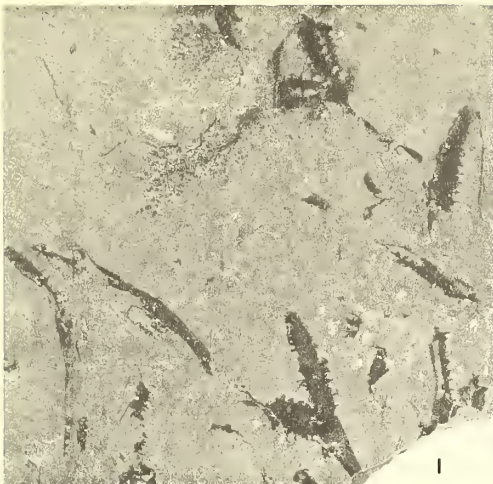
Krithodeophyton croftii sp. nov.

PLATE 130, figs. 1–12; Plate 132, figs. 1–10

Diagnosis. Plant, at least 10·0 cm. high, consisting of naked, pseudomonopodially branching axes, 1·5–4·3 mm. wide, with some dichotomous branching in the distal parts; wide angles ($< 80^\circ$) at branching points. Small bud-like lateral branches about 4·0 mm. long. Simple, circular protostele, average diameter 0·5 mm., composed of mainly scalariform, with some reticulate, tracheids; smallest elements at the centre of the xylem. Outer cortex composed of elongate, thick-walled cells, 36–60 μ in diameter. Epidermis composed of short, fusiform cells. Sporangia aggregated into terminal spikes, 2·5–3·0 mm. wide and up to 1·3 cm. long. Dichotomous branching within the base of the fertile region or just below it. Oval sessile sporangia, 1·25–1·5 mm. long and 0·8–1·0 mm. wide borne in two rows, one on either side of the axis. Narrow sterile appendages up to 2·5 mm. long, given off at right angles to the axis, alternate with the sporangia. Bracts straight throughout their length or with distal parts curving downwards. Sporangium wall composed of isodiametric cells, of average diameter 27 μ . Homosporous. Spores approximately circular in outline, average diameter is 60 μ ; simple trilete $\frac{2}{3}$ – $\frac{3}{4}$ of the spore radius long; variable wall elements up to 3 μ high (the majority being under 1 μ); ornament reduced or absent in contact area. Assignable to the dispersed spore genus *Apiculiretusispora*.

EXPLANATION OF PLATE 130

Figs. 1–12. *Krithodeophyton croftii* sp. nov. 1, 4, Rock bearing fertile spikes, $\times 1\cdot1$ (V26578 and V26579 respectively). 2, 5, Sterile axes, $\times 0\cdot9$ (V52154 and V52152 respectively). 3, Film pull showing epidermal cells, $\times 80$ (V52151, BMP 25). 6, Film pull from axis showing small lateral branch. (Inset = specimen before treatment), $\times 6$ (V52154, BMP 12). 7, Film pull from axis showing cortical cells, $\times 50$ (V52144, BMP 1). 8, Central strand after treatment with Schulze's solution, $\times 200$ (V52137, BMM 22). 9, Central strand on film pull, $\times 100$ (V52145, BMP 2). 10, T.S. axis showing xylem strand before a division, $\times 108$ (V52150, RS1/8). 11, T.S. pyritised xylem strand with centre not preserved, $\times 108$ (V52138, RS1/4). 12, T.S. part of outer cortex, $\times 108$ (V52150, RS1/5).



EDWARDS, Lower Old Red Sandstone plants

Locality. Brecon Beacons Quarry, abandoned roadside quarry on the A470 between Brecon and Merthyr, approximately $7\frac{1}{2}$ miles south of Brecon.

Horizon. Senni Beds, Breconian, Lower Old Red Sandstone of South Wales ($\equiv$ Siegenian).

Holotype. Specimen V26579, Department of Palaeontology, British Museum (Natural History), London.

Description of vegetative parts. The over-all height, branching frequency, and basal parts of the plant are unknown. The most complete fertile specimen found was 10 cm. long, with axes 2 mm. in diameter. There were two branching points (3.4 cm. apart) in the vegetative region, and a further dichotomy occurred within the base of the spike of sporangia. The diameter of the sterile axes ranged between 1.5 and 4.0 mm. and axes of similar size were always found together. Hence it is probable that larger ones formed the basal, and small axes the more terminal, parts of the plant. Branching was pseudo-monopodial in these wider axes, and the narrower 'lateral' branch formed a wide angle with the 'main' axis (Pl. 130, fig. 2). These axes tended to be slightly flexuous and, in addition to a central line, 0.5 mm. in diameter, faint longitudinal striations were sometimes visible. Small, lateral bud-like structures up to 4.0 mm. long, which tapered in width from base to apex were also present (Pl. 130, fig. 6). Each was supplied with a central strand of xylem. The axes associated with the fertile regions were much narrower (< 20 mm. wide) and branched dichotomously.

Film pull and maceration preparations revealed some cellular detail of the outer layers of the axes. The outer cortex was the tissue most frequently recovered and consisted of very long cells with thick walls, 36–44 μ apart. Occasionally the tapering, overlapping ends of these cells were seen (Pl. 130, fig. 7). Scattered among the thick parallel walls were thinner, irregular lines probably representing the remains of underlying tissue. The outer cortical cells were represented in the transverse sections of petrified axes by 1 or 2 layers of angular cells (35–60 μ in diameter) surrounding a structureless mass of pyrites, containing a circular protostele. The outer walls of the cortical cells were often broken down giving the surface of the axis a hairy appearance (Pl. 130, fig. 12). In one instance only, a piece of cuticle was found where the cells had thinner walls, were fusiform in shape and relatively short (Pl. 130, fig. 3). It is probable that this was the epidermis.

The central strand of xylem was composed mainly of scalariform tracheids in which pits on adjacent walls were opposite (Pl. 130, figs. 8 and 9). A few elements showed reticulate pitting. Sections through petrified xylem revealed similar anatomy. The central part was usually not preserved (Pl. 130, fig. 11), but a decrease in tracheid diameter from the outside of the xylem inwards was always apparent. In a few cases, very small elements could be seen at the centre. The protoxylem is therefore considered to be central. The largest tracheids measured 35 μ in diameter and the distance between the horizontal bars of the scalariform tracheids was sometimes as great as 10 μ .

In one axis only could stages in the division of the xylem be seen. A few millimetres below the branching point, the xylem became oval in cross section (Pl. 130, fig. 10) and divided to give two circular strands of approximately the same diameter. The axis itself then divided into two.

I have found well-preserved pyritised axes with similar anatomy to those described above at the same locality. I include a detailed account of them here to emphasize this

close anatomical and morphological similarity, but in the absence of any reproductive parts in the new specimens, I feel it would be unwise to conclude that the two sets of remains belong to the same plant.

The axes were at least 10.0 cm. long and 2.0–3.0 mm. wide. They branched dichotomously and were slightly flexuous. One axis bore a small protuberance 2.0 mm. long and 1.5 mm. wide (Pl. 131, fig. 1) comparable to the small lateral branch in *Krithodeophyton*. The surfaces of the axes were striated. Film pulls showed thick longitudinal walls similar to those described above and sometimes smaller fusiform cells were seen (Pl. 131, fig. 4).

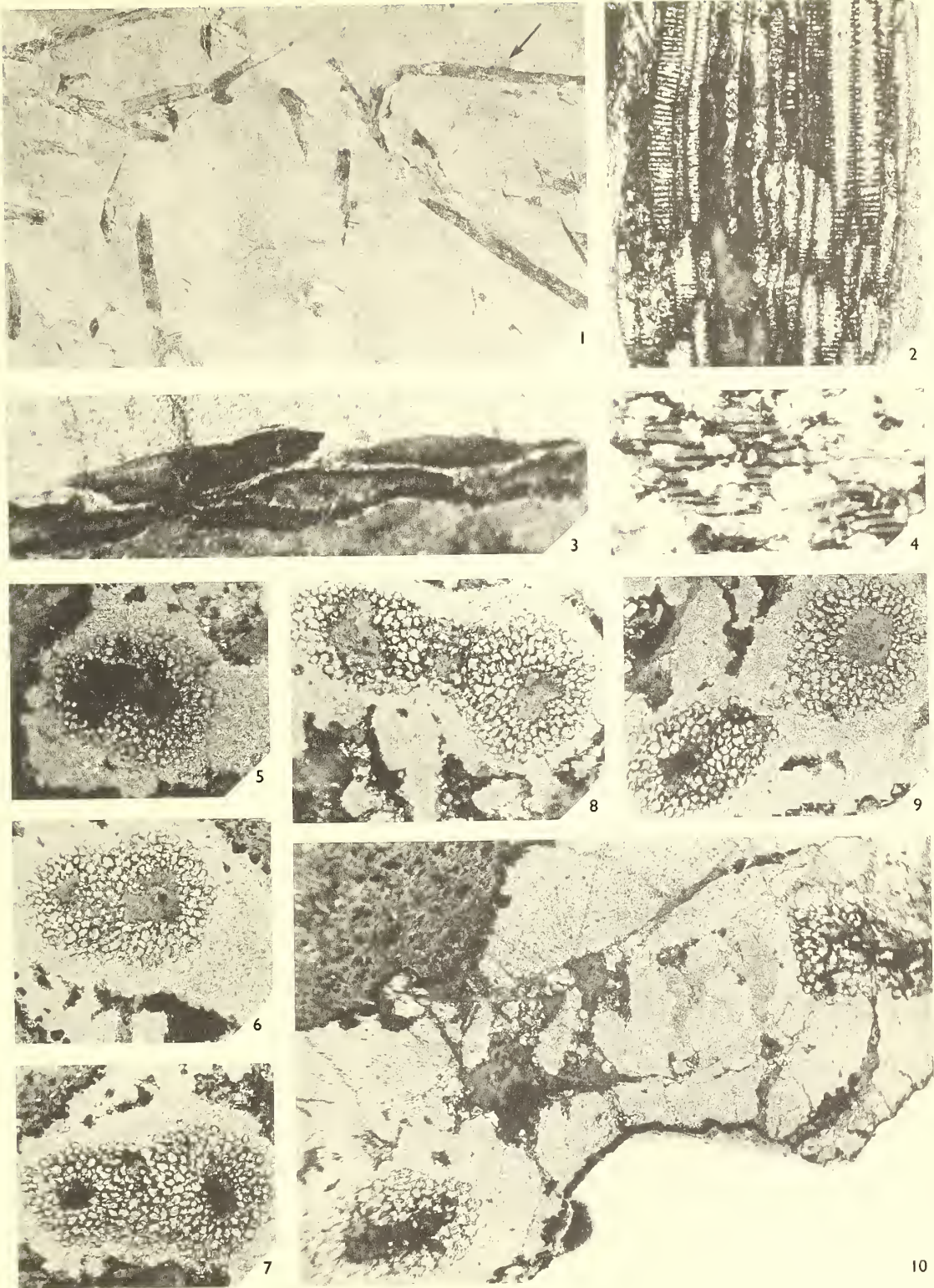
Transverse and longitudinal sections through petrified axes showed a circular protostele composed predominantly of scalariform tracheids (Pl. 131, figs. 2 and 5). Some reticulate pitting was seen. The widest tracheids were found to the outside of the xylem. The cells at the centre were either not preserved or very small and crushed (Pl. 131, fig. 5). Immediately outside the xylem was a narrow band of squashed thin-walled cells. One or two layers of thick-walled cells, circular to angular in cross-section, with an average diameter of 49 μ , formed the outermost layer of the axis. The outer walls of these cells were eroded away so that the radial walls project into the matrix, giving the axis a hairy outline (Pl. 131, fig. 6) which is also seen in *Krithodeophyton*. In longitudinal sections, the cortical cells had tapering ends (Pl. 131, fig. 3). They were, on average, 350 μ long.

Stages in the division of the xylem below a branching point are illustrated in Plate 131, figs. 5–10.

Description of fructifications. The sporangia were aggregated into terminal spikes. A few millimetres below the fertile region an axis dichotomised and this was followed by a further dichotomy immediately below or within the base of the fructification (Pl. 130, fig. 4). Isolated fructifications were common in the matrix (Pl. 130, fig. 1). The spikes were at least 1.3 cm. long and, on average, were 2.75 mm. wide. The majority were incomplete at the apex and 6.0–8.0 mm. long. At the base they were parallel-sided, but there was a gradual decrease in width in the distal parts and the apices were rounded (Pl. 132, fig. 4). No organization was apparent in the distal parts. The sporangia were oval in outline, 1.25–1.5 mm. long and 0.8–1.0 mm. wide (Pl. 132, fig. 2). They were sessile on a central axis (0.3 mm. diameter) which was often obscured by the sporangia themselves. The sporangia appeared to be arranged in two rows one on either side of the axis, each row containing at least eleven sporangia. It is unlikely that this arrangement was produced by compression of an originally spiral or whorled organisation as the sporangia are quite distinct. At the base of the spike the long axes of the sporangia were orientated at right-angles to the central axis, in the distal part they were directed toward the apex. Alternating with the sporangia and extending beyond them out into the matrix were thin, possibly spine-like appendages up to 2.5 mm. long (Pl. 132, figs. 3 and 5).

EXPLANATION OF PLATE 131

Figs. 1–10. *Krithodeophyton croftii* sp. nov. 1, Branching sterile axes from Brecon Beacons Quarry (small lateral projection indicated by arrow), $\times 1$ (DE 32/1). 2, Section through petrified axis, L.S. xylem strand composed of scalariform tracheids, $\times 108$ (32–4–33). 3, As last, L.S. outer cortical cells, $\times 108$ (32–4–35). 4, Film pull of surface of axis showing epidermal cells, $\times 80$ (DE32. P77). 5–10, Series of sections of petrified axis showing division of xylem at a branching point, $\times 51$ (Series 32–4).



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These arose at right angles to the fructification axis and sometimes curved downwards at their tips. The exact relationship between sporangium and lateral appendage or bract could not be determined with certainty as the structures were very heavily carbonised. In some cases, the base of a sterile bract extended down the central axis partially covering the sporangium below, giving the impression that the sporangium and the bract above it formed a single unit (Pl. 132, fig. 1). Plate 132, fig. 2 shows a fructification, where sporangia only are visible, while in Plate 132, fig. 6 only bracts are present. Where sporangia and bracts were slightly superimposed the sporangia appear beaked. At the moment it seems very likely that the appendages were not attached to the sporangia, but that both were borne separately on a central axis.

Description of spores. Maceration and film pull preparations showed spores adhering to the sporangium wall. The cellular structure of the walls was not preserved, but some very fragmentary remains indicated that part of the wall was composed of isodiametric cells, around $27\ \mu$ in diameter. Imprints left by the spores could frequently be seen in the sporangium wall (Pl. 132, fig. 7). A small number of spores were recovered by dissolving the film pull bearing a sporangium (Pl. 132, figs. 8–10). They were all approximately the same size, with an average diameter of $58\ \mu$ (range: 55 – $68\ \mu$). The spores were almost circular in outline. The position of the trilete was usually difficult to establish because of heavy folding, but in one case a simple Y-mark was observed. The length of the trilete was almost equal to the spore radius. The wall ornament was made up of rather variable elements ranging from coni to spinae, which were $1\ \mu$ or less high. Narrower parallel-sided elements with truncated tips occasionally reached a height of $3\ \mu$. There was a well-developed contact area, where the ornament was much reduced or absent. These spores are assignable to the dispersed spore genus *Apiculatiretusispora* (*sensu* Streel 1964) and are comparable to the species *A. brandtii* (Streel 1964).

In conclusion it must be emphasized that no anatomy has been detected in the axes attached to the fertile regions. The sterile and fertile parts are thought to belong to the same plant because they are always found in close association, no other plant being present, and where fructifications terminate relatively long axes, the latter have the same dimensions, surface features, and branching angles as do the sterile axes.

Discussion. Plants with a similar arrangement of sporangia in terminal spikes and, in some cases, with sterile and fertile appendages intermixed, are known from other Devonian deposits. These include *Barinophyton*, *Protobarinophyton*, *Pectinophyton*, and the possible reproductive parts of *Enigmophyton*. Høeg (1942) described some fertile axes, which he considered were probably attached to *Enigmophyton superbum*. These plants came from the upper Middle Devonian of Spitzbergen. As in the Welsh plant, the sporangia, which alternated with sporophylls, were arranged in two rows, with dichotomous branching occurring both below and within the base of the fructification. Høeg, however, thought that the two rows were produced by compression of an originally verticillate or spiral arrangement of appendages. He considered the sporangia to be borne proximally on the upper surfaces of the sterile bracts. Unlike *Krithodeophyton*, this plant was heterosporous, and Vigran (1964), described the spores in detail. She identified the microspores as *Phyllotheocotrilletes microgranulatus* (average diameter $72\ \mu$) and called the megaspores *Enigmospora simplex* (200 – $70\ \mu$ diameter). Although the microspores are comparable in size to those spores isolated from *Krithodeophyton*, the

ornament is quite different. Nothing resembling the fan-shaped leaves of *Enigmophyton superbum* has been found at the Brecon Beacons Quarry.

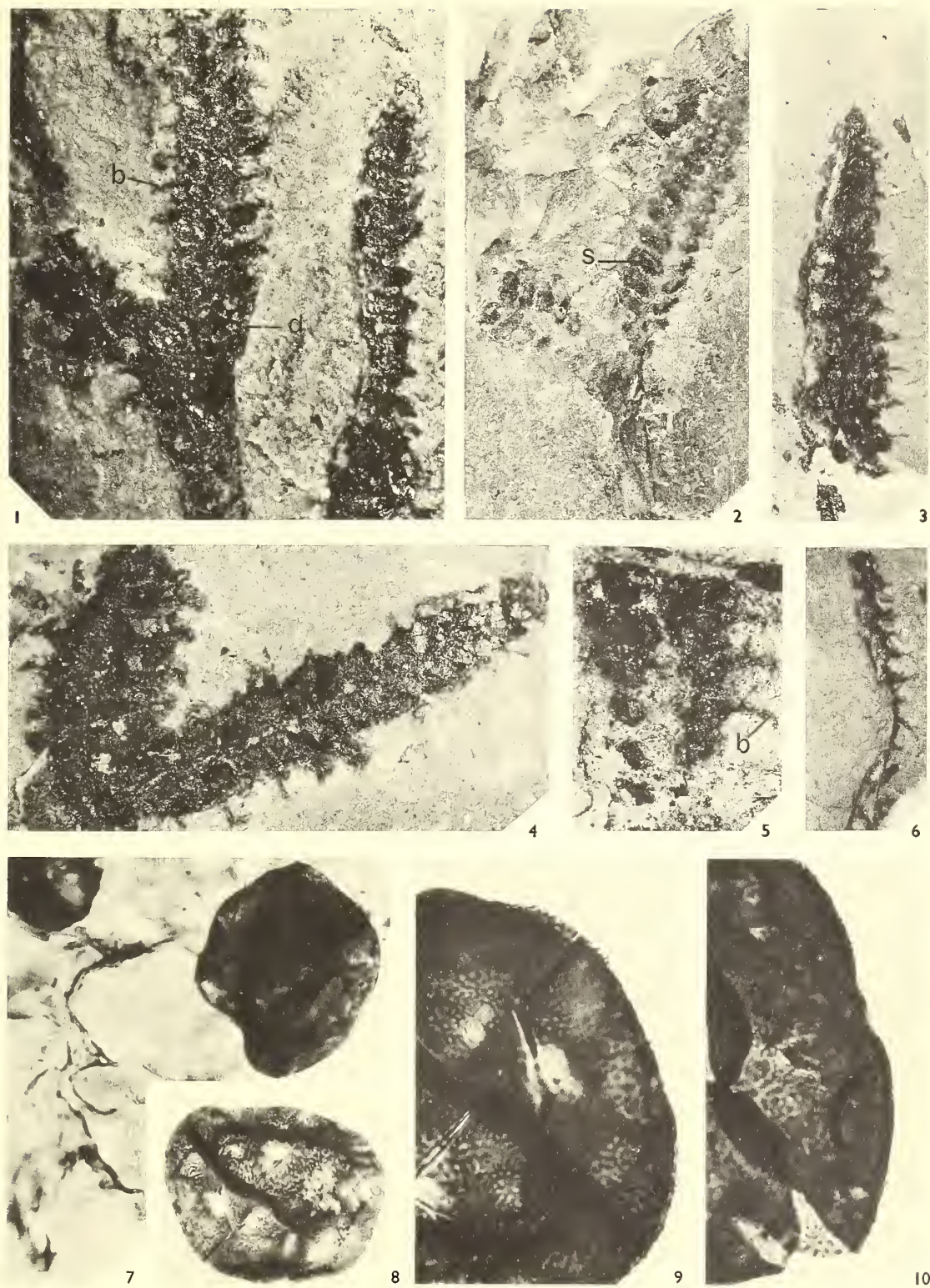
Earlier, Høeg (1935) had described a Middle Devonian plant from Norway, in which naked axes, with mainly pseudomonopodial branching had fructifications terminating the 'lateral' branches. The sporangia, or perhaps the organs bearing the sporangia, were arranged in two rows, both borne on the lower surface of the fructification axis. Høeg called this plant *Pectinophyton norvegicum* and Ananiev (1957), described another species *P. bipectinatum*, where the axis of the fructification bore two rows of long, lateral appendages, twisted towards the axis. On the inside of the resulting coils were attached the sporangia. The axis had a central strand of annular tracheids. Whereas Petrosyan, in Lepekhina, Petrosyan, and Radchenko (1962) considered the above two species to be identical, Høeg (1967) maintained that they were two distinct species on the basis of differences in sporangial shape and arrangement. Not enough is known of Høeg's plant to make a satisfactory comparison with *Krithodeophyton*, but *P. bipectinatum* with its apparently complex organisation in the sporangial region, is quite unlike the Welsh plant.

The genus *Barinophyton* was erected by White (1905), when he re-investigated some plants from the Upper Devonian of Perry, Maine. He distinguished three species, *Barinophyton richardsonii* (*Lepidostrobus richardsonii* Dawson 1861, *Lycopodites richardsonii* Dawson 1863), *B. obscurum* (*Pecopteris* (?) *obscurum* Dun 1898), and *B. perryanum*. The most completely described species in the literature are *B. citrulliforme* from the Upper Devonian of New York (Arnold 1939) and *B. richardsonii*, re-described by Pettitt (1965). Arnold showed that branching in the sterile region was pseudomonopodial but that the fructifications, much larger than in *Krithodeophyton*, terminated lateral branches. In both *Barinophyton* species the fructification axis bore on its dorsal surface two rows of appendages between which were found the sporangia. They were unlike *Krithodeophyton* in that the appendages did not extend beyond the sporangia and were discoidal in shape. In addition, in Pettitt's re-construction two sporangia occurred between successive bracts in each row. Where the sporangia were borne in two rows, one on either side of the fertile axis, i.e. the normal *Krithodeophyton* arrangement, Arnold thought the arrangement was produced during fossilization. Both species were heterosporous. A Middle Devonian species, *B. sibiricum* (Lepekhina *et al.* 1962) differed from the Welsh plant in having long, lax, pendant spikes of sporangia.

In 1954, Ananiev described *B. obrutschewii* from the Lower Devonian of the U.S.S.R. This differed from previously described species of *Barinophyton* in that branching was dichotomous not pseudomonopodial. On the basis of this difference alone, he transferred the plant to a new genus *Protobarinophyton obrutschewii* (Ananiev 1957). Although in 1954, Ananiev had briefly mentioned sporophylls associated with the sporangia, in later papers by him and other authors no mention is made of them. Certainly *Protobarinophyton obrutschewii* f. *muconata* (originally *Distichophytum muconatum* Ananiev) transferred

EXPLANATION OF PLATE 132

Figs. 1-6. Fructifications of *Krithodeophyton croftii* sp. nov.; s, sporangium; b, bract; d, branching within the base of the fertile region. 1, $\times 5$ (V26579). 2 and 6, $\times 2.3$ (V26578). 3-5, $\times 5$ (V26578). 7, Sporangium wall with spores attached, $\times 500$ (V52146, BMS 12). 8-10, Spores isolated from sporangia. 8, $\times 500$ (V52146, BMS 1). 9 and 10, $\times 1000$ (V52146, BMS 1).



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to the genus by Lepekhina *et al.* (1962) had no bracts in the fertile region. Ananiev (1963) stated that the sporangia of *P. obrutschevii* contained spores of one size only (70 μ diameter).

Krithodeophyton and *Protobarinophyton* resemble each other in many ways. Indeed, considering such characters as their similar age, the aggregation of oval, sessile sporangia into terminal spikes, homospority and dichotomous branching in the fertile regions, they might be included in the same genus. However, until more is known of the detailed organization of the spikes (e.g. whether or not bracts are present), about the spores and the anatomy of the axes of *Protobarinophyton*, I feel justified in erecting a new genus for the Welsh plant. Differences include the absence from *Krithodeophyton* of U- and H-branching, the absence of dehiscence lines on the sporangia and the presence of scalariform not annular tracheids in the protostele. In addition, the spikes in *Krithodeophyton* were much smaller, more compact and had distinctly protruding bracts. The specimen illustrated in Plate 132, fig. 2, in which no bracts are visible, most closely resembles the Russian plant. It is possible that this specimen represents a late stage in the maturation of a spike, where the sporangia were large and completely obliterated the bracts. This explanation could be applied to the apparently bractless condition seen in *Protobarinophyton*. Variation within the species has been indicated by Lepekhina *et al.*, who distinguished a *P. obrutschevii* f. *minuta* from *P. obrutschevii* f. *typica*, but little is known of the variation in fructification morphology within a single population.

In conclusion it is stressed that not enough is known of the details of anatomy and morphology of any of the plants discussed above. It may be that ultimately they will all be placed in the same genus. Indeed Arnold believed that this was true for *Pectinophyton* and *Barinophyton*. On the information available at the moment, I propose to place this relatively completely described Lower Devonian plant in the new genus *Krithodeophyton* (Derivation: *Krithodes*—like barley).

Classification. Ananiev (1963) included *Protobarinophyton*, with *Zosterophyllum* and *Bucheria* in the Zosterophyllaceae. My own observations on the anatomy of *Z. llanoveranum* show that *Krithodeophyton* is not related to this species, because the latter had an elliptical exarch protostele, and therefore should not be placed in the same family. In his contribution to the second volume of the *Traité de Paléobotanique* (ed. Boureau 1967), Høeg included the Barinophytales as an order, Incertae Sedis, containing two families, Barinophytaceae and Barrandeinaceae. The former included, in addition to *Barinostrobis*, all the genera mentioned above with the exception of *Euigmophyton*. It is suggested that *Krithodeophyton* should also be placed in this family.

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D. EDWARDS
Botany School
Downing Street
Cambridge

Typescript received 1 March 1968

DENCKMANNITES (TRILOBITA) FROM THE SILURIAN OF NEW SOUTH WALES

by L. SHERWIN

ABSTRACT. The trilobite *Denckmannites* Wedekind is redefined and a new species, *Denckmannites rutherfordi*, is described from Siluro-Devonian shales near Orange in the Central West District of New South Wales.

THE genus *Denckmannites* has hitherto been recorded only from the Siluro-Devonian of Central Europe and the Devonian of Morocco (Richter, in Moore 1959, p. O 467). The species described in this paper, *Denckmannites rutherfordi*, was found in the Wallace Shale (Stevens and Packham 1952) at a locality about 18 miles west of Orange in the Central West district of New South Wales. The two bands bearing the trilobites were separated by a thickness of 100 ft. of apparently unfossiliferous olive-green shales. Some uncinat monograptids accompanying the trilobites in both bands indicated either a late Silurian, or less probably, an early Devonian age. Other fossils in the lower band include *Dictyonema* sp., *Encrinurus mitchelli* Foerste, an indeterminate odontopleurid trilobite, orthoconic nautiloids, and small orthid and linguloid brachiopods. Apart from *Monograptus* sp., the only associates of *Denckmannites* in the upper band are *Dictyonema* sp. and *Encrinurus* sp.

The morphological terms are as in the Treatise, Part O.

SYSTEMATIC PALAEOLOGY

Order PHACOPIDA Salter 1864

Genus DENCKMANNITES Wedekind 1914

1931 *Phacopidella* (*Denckmannites*) Wedekind; Richter and Richter, p. 143 (cum syn).

1959 *Denckmannites* Wedekind; Richter, p. O 467.

Type species. *Phacops volborthi* Barrande 1852; SD Vogdes 1925.

Emended diagnosis. Cephalon with broad border and shallow border furrow along posterior edge, both continued antero-laterally as far as axial furrows; border furrow joins axial furrow in front of eye; in front of glabella border is reduced or absent. Margin of cephalon sharp, upper surface meeting doublure at acute angle; 3p and 2p glabellar furrows vestigial, equal in depth, unconnected with axial furrows; 1p furrows initially as deep as axial furrows, becoming much shallower axially. Intercalating ring tripartite, distinct from glabella. Eyes small, of *cryptothalmus* pattern. Entire posterior section of facial suture with forwardly directed convex curvature; genal angles rounded. Vincular furrow crenulate, developed only on postero-lateral doublure. Pygidium large, rounded, with narrow border and smooth surface.

Remarks. In 1914 Wedekind erected the subgenus *Glockeria* (*Denckmannites*) without selecting a type, referring the definition instead to the 'group of *Phacops volborthi* Barrande' which also included *P. miser* Barrande and *P. fugitivus* Barrande. *P. volborthi*

[Palaontology, Vol. 11, Part 5, 1968, pp. 691-6, pl. 133.]

was subsequently designated as the type by Vogdes in 1925; Richter and Richter (1931) confirmed this action by applying Art. 30, 1a of the then current Rules for Zoological Nomenclature. In defining *G. (Denckmannites)* Wedekind stated that the cephalon is totally surrounded by a border. However, this feature is found only in *P. volborthi* and possibly *P. fugitivus*, but not in *P. miser*, although Wedekind included them within his subgeneric conception. In addition, he stated that the 1p glabellar furrows did not coalesce, although they are shown connected in figures of *P. volborthi* and *P. miser* by Barrande (1852). Vogdes (1925) designated *P. volborthi* as the type for *Phacopidella (Denckmannites)*, but retained Wedekind's diagnosis unaltered. Richter and Richter (1931), in revising the subgenus, omitted any reference to the cephalic border and 1p glabellar furrows. They distinguished *Phacopidella (Denckmannites)* from *P. (Phacopidella)* by its 'uniform glabellar surface anterior to the 1p furrows as in *Phacops* (i.e., an undivided glabellar surface with only mere vestiges of 2p and 3p furrows), eyes of a *cryptothalmus* pattern, and a tripartite intercalating ring' (p. 143, in German). Richter (in Moore 1959, p. O 467) raised *Denckmannites* to full generic status, at the same time modifying the 1931 diagnosis by referring to the intercalary furrow as tripartite instead of the intercalating ring. The genal angles were described as truncate, while the entire posterior section of the facial suture was specified as concave; i.e., with the concave side directed posteriorly. Alberti (1966) designated *P. (D.) micromma* (A. Roemer) as the type species for *Phacopidella (Struveaspis)* thus restricting the scope of the genus *Denckmannites* (*sensu* Richter 1959). This new subgenus is characterized by fusion of the reduced central lobe of a tripartite intercalating ring to the base of the glabella by medial reduction of the 1p furrows. For the sake of conformity in the two following lists, *Struveaspis* is regarded as being of the same generic status as *Denckmannites*.

Species retained in genus *Denckmannites*:

Denckmannites volborthi (Barrande) 1852

Denckmannites miser (Barrande) 1852

Denckmannites rutherfordi sp. nov.

Species transferred to *Struveaspis*

Struveaspis micromma (A. Roemer) 1852

Struveaspis fugitivus (Barrande) 1872

Struveaspis thuringica (Kegel) 1932

Struveaspis prantli (Růžička) 1946

Struveaspis n.sp. A. Alberti 1966

Denckmannites rutherfordi sp. nov.

Plate 133

Source of name. After the Rutherford family, on whose property the fossils were found.

Material. Six more or less complete exuviae preserved as internal moulds with fragments of the exoskeleton adhering; USGD (University of Sydney Geology Department) 8914, 8916, 8934, and MMF (Geological and Mining Museum, Sydney) 14467. The external counterparts of USGD 8929 and 8934 have also been preserved. The only deformation is that caused by burial pressure, with crushing of the glabella. In addition, abundant imperfect specimens were also collected from the same locality.

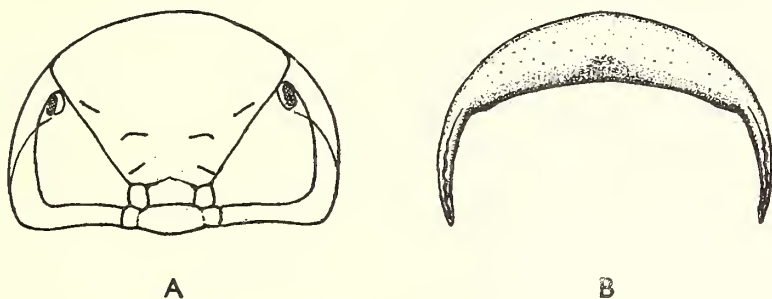
Holotype. USGD 8927 a, b.

Paratypes. USGD 8929, 8934, MMF 14467.

Locality. Portion 216, Parish Boree Nyran, County Ashburnham.
Sydney University Geology Department Locality catalogue MN/II/27.

Diagnosis. *Denckmannites* with very small eyes (about 20 lenses in each), deep transglabellar 1p furrows becoming shallow axially, and exceedingly narrow anterior cephalic border; pygidium with 6–7 discrete axial rings.

Description. The carapace possesses a long oval outline and, except for a strongly convex axis, has only moderate relief. The cephalon has a micro-granulose surface and a semicircular outline, with rounded genal angles which do not project noticeably beyond its posterior edge. The interior of the cephalon is pitted. The wide border is defined by a shallow border furrow, and is continuous along the posterior and lateral



TEXT-FIG. 1. A. Reconstruction of cephalon showing inferred position of facial sutures. B. Reconstruction of ventral surface of cephalon, showing approximate shape of doublure.

edges of the cephalon, maintaining a more or less uniform width. In front of the glabella the border narrows considerably; none of the specimens was sufficiently well preserved to determine if it disappears altogether. The border furrow runs parallel to the margin as far as the anterior corner of the cheeks, where it swings sharply into the axial furrow. Anterior to the 1p furrows the axial furrows are straight, and are generally deeper than the border furrow. Near the cephalic margin they fade, and outline the glabellar curve to the edge of the cephalon before disappearing entirely.

The glabella is large, pentagonal, and slopes forward gently to meet the doublure in an acute angle. The 2p and 3p furrows are weak, and do not meet the axial furrows. In different specimens the 2p furrows are represented by straight or curved furrows, the curve always being directed anteriorly. The posterior branches of the 3p furrows are generally more strongly curved than the 2p furrows; the 3p anterior branch is straighter and inclined at about 30 degrees to the axial furrows. The 1p furrows cut deeply into the glabella for about one-third of their length, where they divide into two branches. The anterior branches swing forward decreasing in depth, being joined axially by a shallow depression. The posterior branch cuts the intercalating ring and joins the occipital furrow. The intercalating ring is thus trisected into a broad medium lobe and two ovoid lateral lobes. This division is reflected by the vaguely tripartite occipital ring. The cheeks have a slightly lower relief than the glabella; approximately triangular in shape, they support very small eyes at their anterior corners. Preservation does not indicate whether an anterior section of the facial suture exists or not; the posterior section has a forwardly directed curvature throughout, and intersects the cephalic margin just in front of the genal angles.

The eyes are oval in shape, supported on a reniform palpebral lobe. Preservation does not allow an accurate count, but each eye probably has between 19 and 21 lenses arranged in six vertical rows as follows (front-rear): 2, (?3), 3, 3, (?4), 4, 4, 3. In the holotype (USGD 8927) a portion of the exoskeleton partially covering one of the eyes shows no expression of the underlying lenses, unlike other species even in the same genus where the lenses are quite prominent surface features. Unless the exoskeleton in this region was transparent, it seems unlikely that the eyes could have functioned as light sensitive organs.

The hypostome is triangular in shape with a slightly convex anterior margin. The anterior wings are particularly well developed, with appreciable thickening at their tips. On the ventral surface there is a small longitudinal ridge which runs from the lateral notch, fading at the anterior margin: on the dorsal surface the ridge is expressed as a shallow furrow. The border is continuous posterior to the lateral notches, and is broadest along the posterior edge. Any other details of the posterior border were obscured in all specimens by either cephalon or thorax. The median body is subcircular, apparently undivided, and strongly convex. No maculae were observed. The entire surface of the hypostome is finely granulose.

The cephalic doublure is crescentic in shape, broadest beneath the glabella, with a paraboloid posterior margin which commences near the genal angles and passes just behind the eyes. The crenulate vincular furrow is widest near the genal angles, tapers forward, and disappears near the axial furrow. The doublure on small specimens seems comparatively rigid, as in such cases the posterior portion of the glabella, and to a lesser extent that of the cheeks, is crushed along an arc corresponding to the portion of the cephalon unsupported by the doublure. In large specimens, crushing of the cephalon is quite independent of the doublure. As regards ornament, the doublure seems comparable to the dorsal cephalic surface.

The thorax is virtually parallel-sided, showing an appreciable taper in only the last three segments. The axial rings are strongly convex, and have a tripartite division into a central lobe, flanked by smaller, globose, lateral lobes. The central lobe carries a particularly well-formed articulating half-ring, separated from it by a deep but broad transverse furrow. At the junction of central and lateral lobes, the extension of this

EXPLANATION OF PLATE 133

Denckmannites rutherfordi sp. nov.

Figs. 1, 2, 5, 8, 9. Holotype USGD 8927. 1, composite internal mould of cephalon, showing eye covered by exoskeleton which gives no indication of underlying lenses, $\times 5$. 2, Composite internal mould of cephalon, $\times 1.5$. 5, hypostome, $\times 3$. 8, Composite external mould of cephalon, and internal mould of thorax and pygidium. Short hooks are visible on the fragments of exoskeleton adhering to the pleural extremities. 9, Silastic cast of external mould and hypostome, $\times 1.5$. The anterior granulation is caused by pitting on the interior surface of the exoskeleton.

Fig. 3, Paratype MMF 14467. Internal mould exhibiting phacopid or Salterian mode of moulting, $\times 2$.

Fig. 4, Paratype USGD 8934. Latex cast of external mould, showing border and interpleural furrows on pygidium, $\times 1.5$.

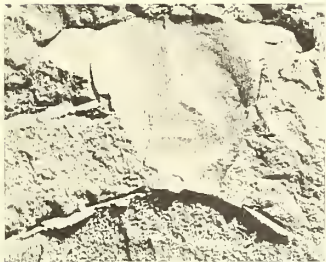
Figs. 6, 7, Paratype USGD 8929a, b. 6, Internal mould, showing crushing of portion of cephalon unsupported by doublure, $\times 3$. 7, Interior of dorsal carapace showing apodemes, $\times 3$. An attempt to make a latex cast resulted in damage to the exoskeleton.



1



2



5



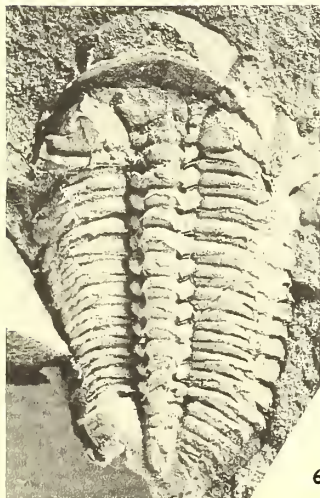
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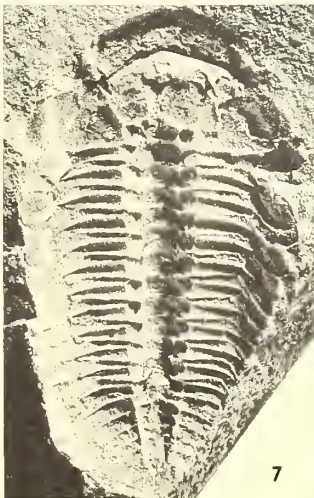
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9



6



7



8

furrow projects downward to form a robust apodeme. These apodemes are flange shaped and taper downwards, with a slight expansion at their tips. The pleurae are more or less uniform in width throughout their length, with deep pleural furrows extending from axial furrow to articulating facet. These facets are large, extending about one half the length of the leading edge and a third the length of the posterior edge of the segments. The first five segments have rounded extremities; the remaining six show progressive development of a short spine or hook, possibly a feature associated with enrollment.

The pygidium has a very rounded outline, marked by a flat border. On internal moulds this border is exaggerated by the imprint of the doublure which extends about one-third the distance across the pleural region. Articulating facets occupy about half the length of the leading ribs. The axis contains six discrete axial rings, a seventh vaguely discernible in some specimens, followed by a fused terminal piece. The first ring is partially obscured by the last thoracic segment. Both the first and second rings are transversely tripartite, though the division is much less pronounced than in the thoracic axial rings. Each pleural field bears five rather flattened ribs, separated by straight and narrow pleural furrows. Interpleural furrows are seldom observed except on external moulds, and are parallel to the pleural furrows. The surface is free of ornament.

Dimensions (in mm.). Holotype USGD 8927:

	<i>Width</i>	<i>Length</i>
Cephalon	22	12
Thorax	24	20
Pygidium	17	9

Remarks. The bohemian species, *Denckmannites niser* (Barrande), most closely resembles *D. rutherfordi*, but has much larger eyes, and the 3p glabellar furrows, as shown in Barrande's illustrations, appears to be whole, not bipartite. *D. volborthi* (Barrande) has eyes of about the same size, with a similar number of lenses in each, as *D. rutherfordi*, but its cephalon is wholly surrounded by a border, while the pygidium has almost twice as many axial segments as *D. rutherfordi*.

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L. SHERWIN

Geological and Mining Museum
36-64 George Street North
Sydney, New South Wales, 2000
Australia

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MORPHOLOGY AND FUNCTION OF DICHOPORITE PORE-STRUCTURES IN CYSTOIDS

by C. R. C. PAUL

ABSTRACT. The cystoids, a diverse and artificial group of extinct Palaeozoic echinoderms, are characterized by the possession of pore-structures developed in the thecal wall and composed of thecal canals which open in thecal pores. Thecal canals may occur singly to form dipores, or in sets perpendicular to plate sutures to form rhombs. Five basic types of pore-structure are recognised: *pectinirhombs*, *cryptorhombs*, *humatirhombs*, *humatipores*, and *diplopores*. The first two are composed of dichopores, thecal canals which connect external pores and through which sea-water flowed in life. The dichopores of pectinirhombs open in slits; those of cryptorhombs open in pores, one of which is sieve-like. Pectinirhombs and cryptorhombs are characteristic of, and confined to, the super-families Glyptocystitida and Hemicosmitida respectively; humatirhombs characterize the superfamily Caryocystitida. Five types of pectinirhombs and one type of cryptorhomb are recognized.

Pectinirhombs and cryptorhombs agree closely with the paradigm of an exchange system and were respiratory structures. Evolution of pectinirhombs proceeded from less to more efficient types independently in all families of Glyptocystitida. The three rhombiferan superfamilies probably acquired their rhombs independently. Rhombifera and Diploporita are regarded as separate classes. The former contains two Orders: Dichoporida and Fistuliporida.

THE cystoids, an extinct group of Palaeozoic echinoderms, are characterized, *inter alia*, by the possession of pore-structures in the calcareous wall of the theca. Although various authors from Müller (1854) to Regnéll (1945) and Kesling (1963) have emphasized the importance of these pore-structures in cystoid morphology and taxonomy, they have not been the subject of complete morphological or functional analyses. Stainbrook (1941) and Sinclair (1948) considered the function of pectinirhombs in one genus each and Delpey (1942) the function of pectinirhombs and cryptorhombs. The last-named author suggested that pectinirhombs and cryptorhombs were balancing organs but most authors have accepted a respiratory function for all pore-structures. Functionally all cystoid pore-structures fall into two groups: dichoporite and non-dichoporite. This paper deals with the dichoporite pore-structures (pectinirhombs and cryptorhombs) after a brief review of the morphology of the five basic types of pore-structure recognized. Function in non-dichoporite pore-structures will be the subject of a future paper.

The cystoids of this account correspond to the class Cystoidea of Kesling (1963) but only to the subclass Hydrophoridae of Regnéll (1945). The hydrospires of blastoids and epispires of certain eocrinoids and crinoids are not considered nor are the peculiar pore-structures of paracrinoids like *Comarocystites* Billings. Knowledge of the morphology of cystoid pore-structures has grown piecemeal, virtually every researcher adding some contribution. One result of this is a rather imprecise terminology often related to ill-defined concepts. In reviewing the morphology of pore-structures an attempt has been made to introduce a systematic terminology and to define the concepts upon which this terminology is based. Previous usage has been followed as far as possible. Throughout this account the classification is that of Kesling (1963) unless otherwise stated.

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MORPHOLOGY OF CYSTOID PORE-STRUCTURES

A. GENERAL

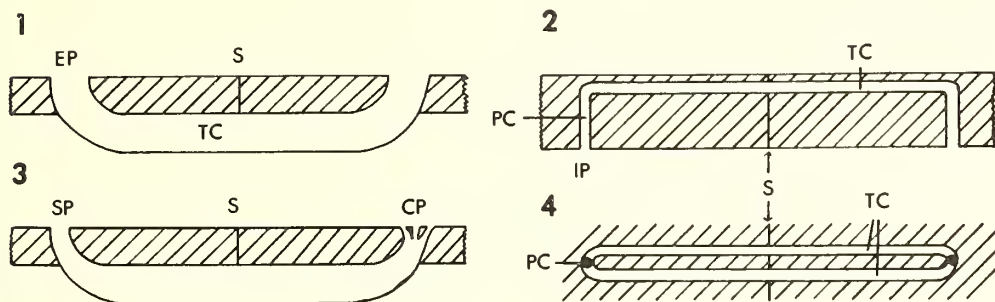
The term *pore-structure* embraces all the structures dealt with. All pore-structures are composed of thecal canals and thecal pores. These have not always been distinguished from each other in the past but Kesling (1963) noted that two separate concepts are involved in the terms pore and canal.

Thecal pores are perforations in the surfaces of the thecal wall. They cannot have a separate existence without the thecal canals to which they give rise, i.e. thecal pores bear the same relationship to thecal canals that the two ends of a stick do to the stick. Pores in the external surface of the thecal wall are *external pores* (text-fig. 1) and correspondingly, *internal pores* (text-fig. 2) are developed in the internal surface of the thecal wall. External pores may be slit-like, and are then referred to as *slits* (text-fig. 12), or they may be either *simple* or sieve-like (text-figs. 3, 20). When simple a single thecal canal terminates in a single pore, when sieve-like the canal divides near the external surface of the thecal wall and opens in a cluster of small pores. Apparently internal pores are always simple and circular in cross-section.

Thecal canals are tubular structures which connect, or terminate in, thecal pores. Thecal canals are analogous to the entire stick plus its ends. The portions of thecal canals which are approximately perpendicular to the surface of the thecal wall are termed *perpendicular canals* (text-fig. 2) and those tangential to the surface, *tangential canals* (text-fig. 2). All thecal canals are composed of one or more tangential canals which connect a pair of perpendicular canals and they all commence and terminate in two thecal pores, both of which lie in the same surface of the thecal wall (with the possible exception of haplopores). Tangential canals may be incompletely calcified or uncalcified, i.e. made of soft tissue only as in diplopores, in which case only the pair of perpendicular canals is preserved in fossils. Thecal canals may be *compound* (text-fig. 4) when several tangential canals connect a pair of perpendicular canals, or *simple* (text-figs. 1, 2) when one tangential canal connects the perpendicular canals. Here thecal canals are considered

as functional units rather than morphological units. Portions of canals composed entirely of soft tissue, as is the case with external papulae, are considered integral parts of the canal even though their former existence can only be inferred in fossils.

Previously two types of pore-structures have been recognized: 'pore rhombs' (or more simply and accurately, *rhombs*) and 'diplores'. The latter term has been used in both a specialized and a generalized sense. The new term *dipore* is proposed to cover all types of pore-structures within the Diploporita and *dipopore* is restricted to one type of dipore following current usage.



TEXT-FIGS. 1-4. Thecal pores and thecal canals.

1. Diagrammatic longitudinal section through a pectinirhomb dichopore to show external pores.
2. Diagrammatic longitudinal section through a simple fistulipore to show internal pores.
3. Diagrammatic longitudinal section through a cryptorhomb dichopore to show simple and sieve-like external pores.
4. Diagrammatic plan view of a compound fistulipore with surface layer removed to show two perpendicular canals connected by a pair of tangential canals.

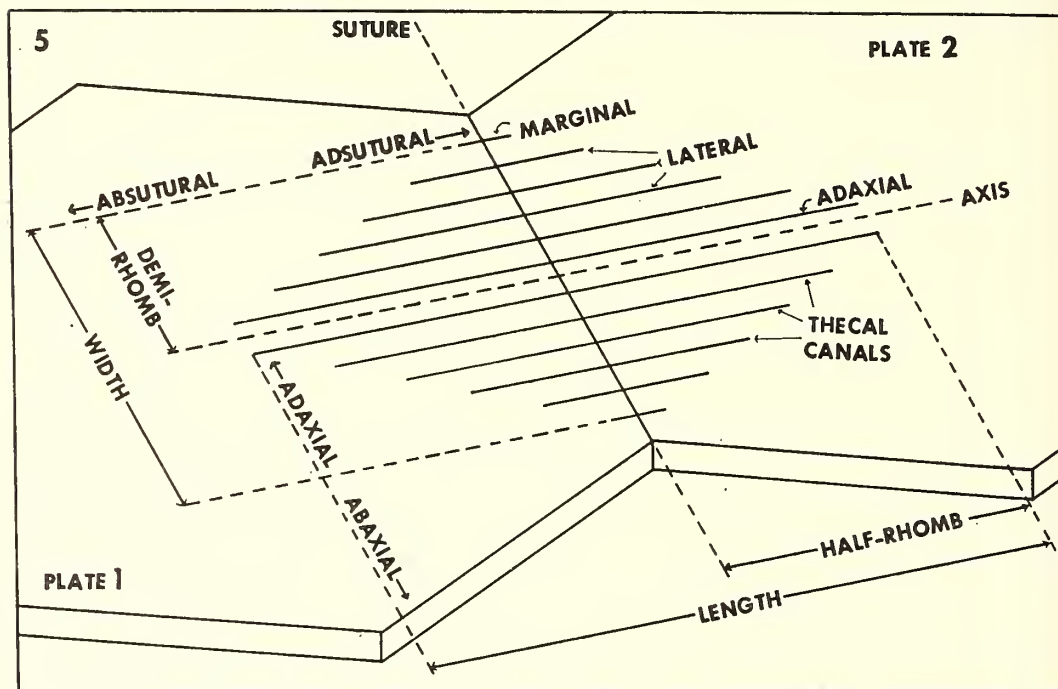
CP, sieve pore; EP, external pore; IP, internal pore; SP, simple pore; PC, perpendicular canal; TC, tangential canal; S, plate suture. In text-figs. 1-3 and all other figures unless otherwise stated, the external surface of the thecal wall is towards the top of the figure.

Rhombs (fig. 5) may be defined as pore-structures composed of a set of thecal canals each of which arises in one thecal plate, crosses a plate suture and terminates in an adjacent plate, the whole set having a rhombic outline in plan view. Rhombs have their thecal canals developed more or less perpendicular to the plate suture and were randomly orientated with respect to other features in the theca since plate sutures occur in almost all possible orientations. Rhombs are therefore orientated and described with respect to their sutures (text-fig. 5).

The outline of a rhomb may be described as indicated in text-figs. 6-11. Rhombs may be composed of two types of thecal canal. Jaekel (1899) proposed the term *dichopore* for the canals (and their terminal pores) of the Rhombifera, Jaekel's *Dichoporita*. Subsequently *dichopore* has been restricted to the canals of pectinirhombs. A fundamental difference exists between canals which terminate in internal pores and those with external pores. No complete canal can have both. Here the term *dichopore* is restricted to rhomb canals with external pores (text-figs. 1, 3) and the new term *fistulipore* (fistula = canal) is proposed for rhomb canals with internal pores (text-figs. 2, 4). There are two types of rhombs composed of dichopores and a third composed of fistulipores. *Pectinirhombs* (text-figs. 15-19) are composed of dichopores which open in slits, whereas *cryptorhombs*

(text-fig. 20) are composed of dichopores which open in pores. *Humatirhombs* are rhombs composed of fistulipores.

Dipores may be defined as pore-structures composed of a single thecal canal randomly orientated with respect to the thecal plates. Dipores are composed of one type of thecal canal, which resembles a fistulipore in connecting internal pores but differs in rarely crossing plate sutures. There were two types of dipore. A *dipopore* is a dipore composed



TEXT-FIG. 5. Diagram of the principal features of a rhomb. Every rhomb is developed in two thecal plates (1 and 2). A plate suture divides the rhomb into two half-rhombs and the width is measured along it. Perpendicular to the suture lies the rhomb axis which divides the rhomb into two demi-rhombs and along which the length is measured. Thecal canals adjacent to the axis are adaxial, those away from the axis lateral and the outermost one or two are marginal. Positions and directions (adsutural, adaxial, etc.) are defined with respect to the plate suture and the rhomb axis.

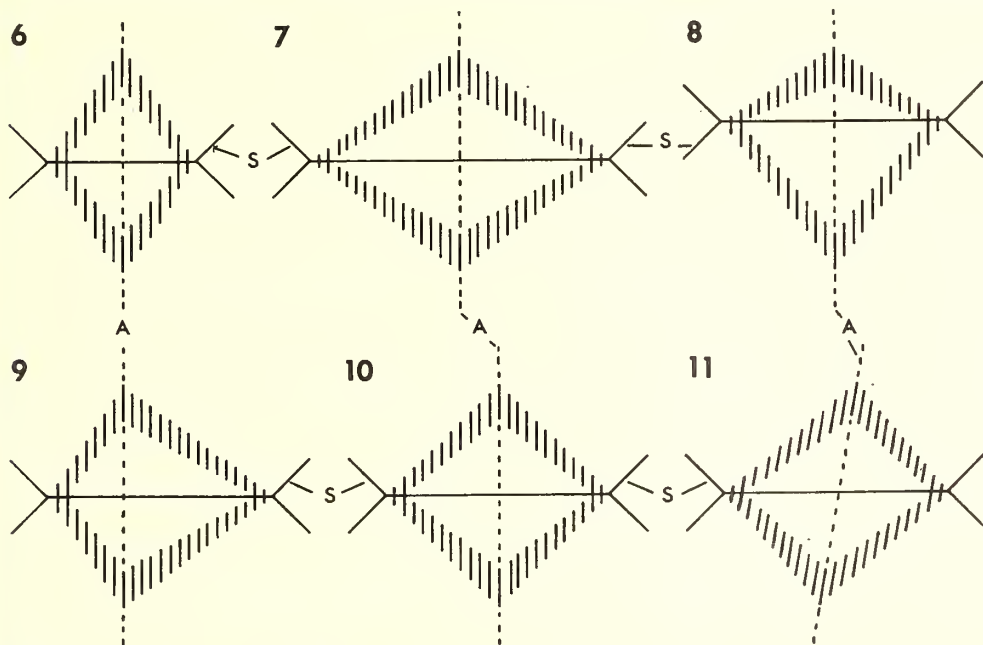
of a simple thecal canal in which the tangential portion was uncalcified, i.e. the tangential portion formed a papula in life and only the two perpendicular portions of the canal are found fossil. *Humatipores* are dipores composed of compound thecal canals in which all the tangential canals were fully calcified.

These five major types of pore-structure are recognized: pectinirhombs, cryptorhombs, humatirhombs, dipopores, and humatipores. The first two differ fundamentally from the other three in that they are composed of thecal canals (dichopores) which connect external pores. Hudson (1911, 1915) recognized this distinction and described dichoporite pore-structures as endothecal and non-dichoporite as exothecal. These general terms may be applied to all types of pore-structures in primitive echinoderms.

A sixth type of pore-structure, haplopores, has been attributed to cystoids. Haplopores,

as here understood, consist of a single, blind (in life), perpendicular canal which opens in a single internal pore. No true haplopores have been observed in any cystoids examined by the writer but this does not imply that none ever existed.

The first information on the structure of the thecal wall, which is intimately related to the morphology of pore-structures, was given by Barrande (1887). Barrande maintained that there were three layers to the thecal wall and that the outer and inner layers sealed



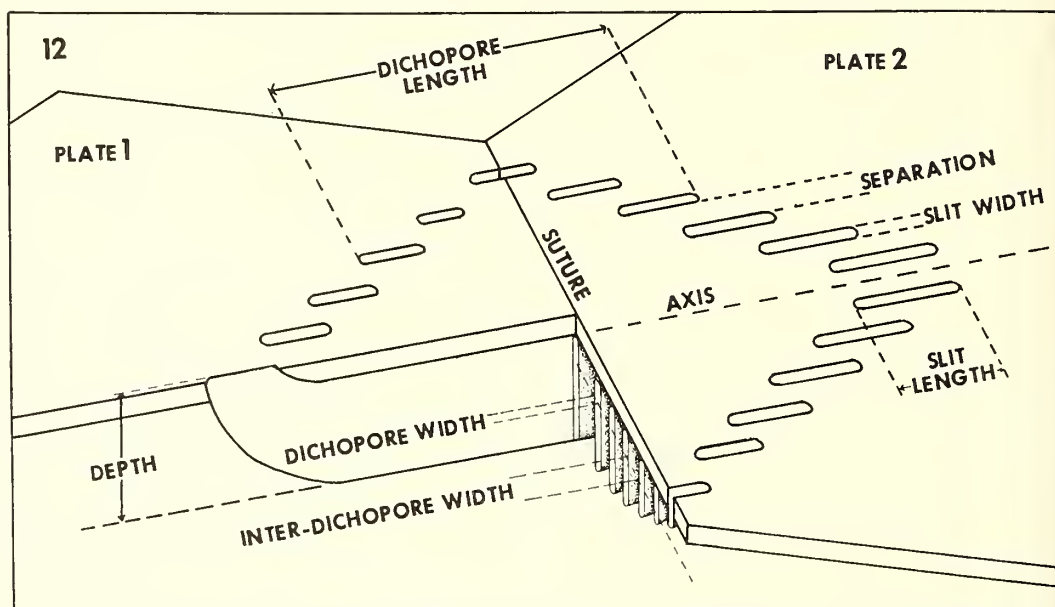
TEXT-FIGS. 6-11. Outlines of rhombs.

Rhomb in which the length exceeds the width are *compressed* (6); the converse, *depressed* (7). Rhombs with unequal half-rhombs are *unequal* (8); the converse, *equal* (6, 7). Rhombs with unequal demi-rhombs are *asymmetrical* (9); the converse, *symmetrical* (6, 7, 8). These features occur in combination. A symmetrical, equal rhomb which is neither depressed nor compressed is *ideal* (10). Rhombs with thecal canals oblique to the suture are *oblique* (11).

A, rhomb axis (an imaginary line); S, plate suture. Text-figs. 6-11 represent disjunct pectinirhombs in plan view but the terms may be applied to all types of rhombs. Rhombs which are 'depressed' into the theca may be termed *sunken* to avoid confusion with those with depressed outlines.

the thecal canals which were confined to the middle layer. Several subsequent authors have described an epithecal layer sealing canals externally but the present writer has found no evidence to support Barrande's statement. Barrande described the surfaces of his layers (as preserved in moulds in most cases) and not cross-sections. All subsequent authors also described surfaces not sections. When the external surface was without pores Barrande claimed an epithecal layer was present; when pores were visible on the external surface he claimed the epitheca was eroded before preservation. However, external surfaces with and without pores may result from the type of canal developed. A rhombiferan with dichopores will have pores in the external surface but one with fistulipores will not *unless* the outer walls of the tangential canals are eroded.

A similar distinction may be made between diploporos, with tangential canals which were of soft tissue and never preserved, and humatipores with fully calcified tangential canals. The description of sealed dichopores in cryptorhombos may possibly result from post-mortem calcification. However, it is more probably due to a misinterpretation of sieve pores as a progressive sealing of the canals. Finally sealed canals do not necessarily indicate the presence of a separate layer sealing them. All thin sections prepared by the author lack any indication of separate layers sealing the canals but the thecal wall is definitely not uniform in structure.



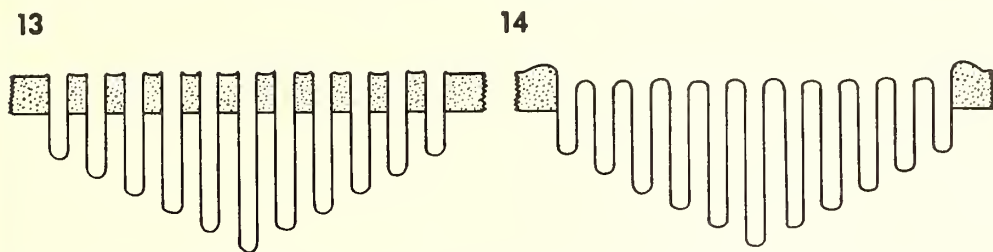
TEXT-FIG. 12. Diagram to illustrate the principal features and measurements of pectinirhomb dichopores and slits. Dichopore and slit lengths and widths are measured in the same direction as rhomb lengths and widths. In this figure and text-figs. 15–20 the external surface of the thecal wall faces the top of the figures and part of the rhomb is removed to show internal features.

B. THE MORPHOLOGY OF PECTINIRHOMBS

Pectinirhombs are rhombs composed of dichopores which open externally in slits (text-fig. 12). The term pectinirhomb was first used by E. Forbes (1848, as 'pectinated rhomb') for the rhombs of the superfamily Glyptocystitida. The various features of pectinirhomb morphology will now be described.

The pores (text-figs. 1, 12) of pectinirhombs are slits. The principal measurements of slits and dichopores are shown in text-fig. 12. There may be a single *conjunct* slit along the entire length of a dichopore (text-figs. 15, 17). Alternatively the dichopore may open in a pair of *disjunct* slits, one at each end (text-figs. 16, 18). One disjunct slit is generally longer than the other and all the longer slits occur in one half-rhomb, a fact first noted by Stainbrook (1941, p. 93) for the pectinirhombs of *Strobilocystites* White. The slit lengths are also approximately proportional to the length of the dichopores to which they give rise and thus marginal slit lengths are less than adaxial slit lengths (text-fig. 32).

The canals (text-figs. 1, 12) of pectinirhombs are dichopores. Pectinirhomb dichopores are *discrete* (text-fig. 13) when each dichopore is a separate entity and the inter-dichopore space is covered by a thin strip of unmodified thecal plate. The inter-dichopore spaces may vary in width in a pectinirhomb with discrete dichopores, and the dichopores open externally in slits each provided with an individual *slit rim*. *Confluent dichopores* (text-fig. 14) are dichopores in which the walls of adjacent dichopores are confluent and the inter-dichopore spaces are covered with dichopore walls. In such cases the inter-dichopore widths are constant and equal to the dichopore widths. Confluent dichopores open in slits grouped into *vestibules* (text-figs. 17, 18) and collectively



TEXT-FIGS. 13–14. Discrete and confluent dichopores.

13. Discrete. Each dichopore is separated from adjacent dichopores by a strip of unmodified thecal plate.

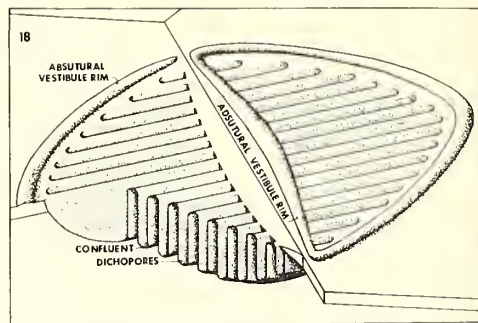
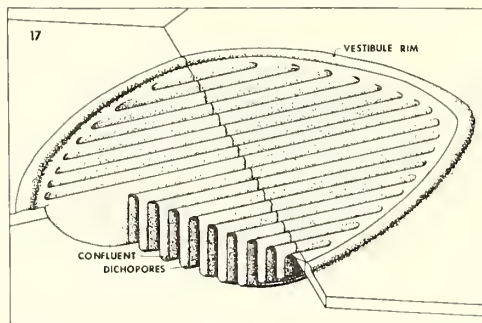
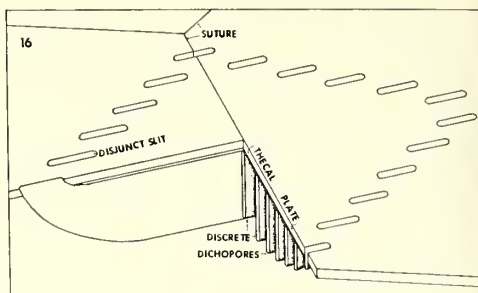
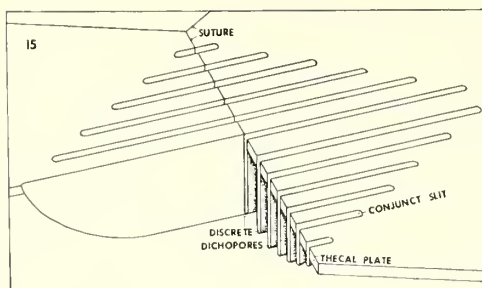
14. Confluent. The walls of adjacent dichopores are continuous and the pectinirhomb is made of isoclinal folds. Both figures represent sutural views of conjunct pectinirhombs.

surrounded by a *vestibule rim*. In disjunct pectinirhombs with confluent dichopores one half-rhomb has a complete *closed rim* which surrounds the slits on both the ab- and ad-sutural sides. The other half-rhomb has an *open rim* on the ab-sutural side only (text-fig. 18). A number of types of pectinirhomb may therefore be recognized on the character of the slits and dichopores. Five types are in fact recognized:

- | | |
|---|----------------|
| 1. Conjunct pectinirhombs with discrete dichopores | (text-fig. 15) |
| 2. Disjunct " " " " | (text-fig. 16) |
| 3. Conjunct " " confluent " | (text-fig. 17) |
| 4. Disjunct " " " " | (text-fig. 18) |
| 5. Multi-disjunct pectinirhombs | (text-fig. 19) |

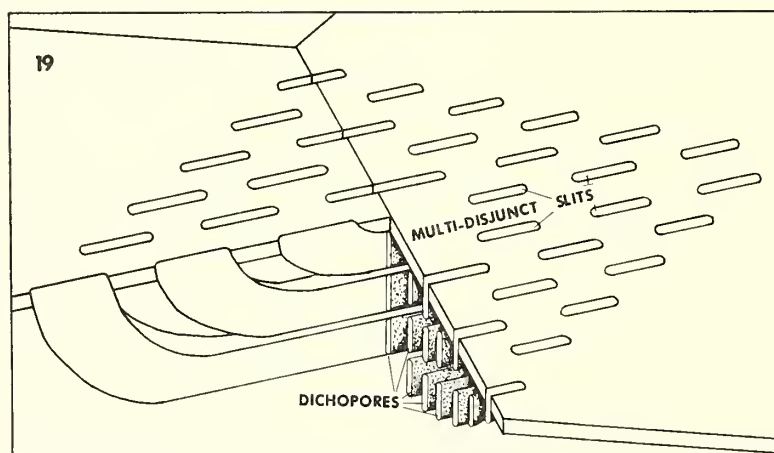
The structure of multi-disjunct pectinirhombs is not yet fully known.

Conjunct pectinirhombs are much less common than disjunct pectinirhombs and discrete dichopores are only found in Ordovician genera. Conjunct pectinirhombs with discrete dichopores are only found in the genus *Cheirocrinus* s.l.: seven species have this type of pectinirhomb. Conjunct pectinirhombs with confluent dichopores occur in the genera *Homocystites* Barrande, *Pleurocystites* Billings, and *Regulaecystis* Dehm. Disjunct pectinirhombs with discrete dichopores occur in the Cheirocrinidae, Rhombiferidae, Cystoblastidae, and Echinoencrinitinae. The Scoliocystinae, Callocystitidae, and *Praepleurocystis* Paul have disjunct pectinirhombs with confluent dichopores. Multidisjunct pectinirhombs occur in two Upper Ordovician species of *Cheirocrinus* s.l., *C. jamesi* (McCoy), and *C. interruptus* (Jaekel). The transition from discrete to confluent dichopores seems to have been gradual and to have taken place independently in several



TEXT-FIGS. 15-18. Diagram to illustrate the morphology of pectinirhombs.

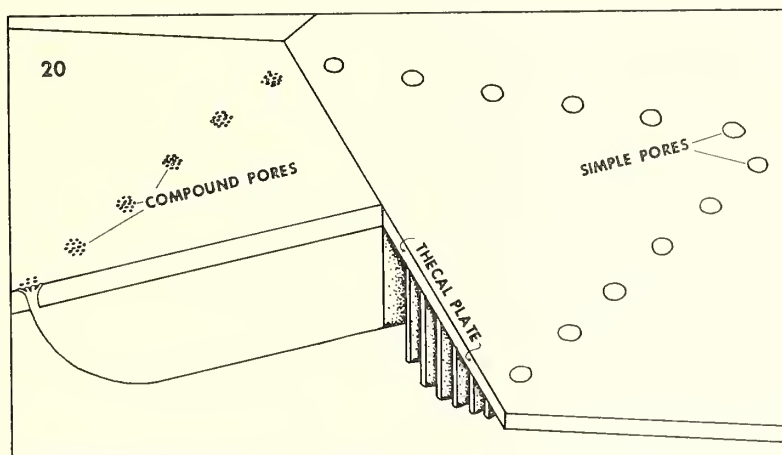
15. Conjunct with discrete dichopores.
16. Disjunct with discrete dichopores.
17. Conjunct with confluent dichopores.
18. Disjunct with confluent dichopores.



TEXT-FIG. 19. Diagram to illustrate the interpretation of the morphology of a multidisjunct pectinirhomb.

families. In particular the pectinirhombs of *Glyptocystites* spp. are intermediate in character. Isolated demi-rhombs only occur in species which have pectinirhombs with discrete dichopores.

All five types of pectinirhomb are confined to and characteristic of the superfamily Glyptocystitida. Members of this superfamily have thecae composed of a definite number of plates arranged in five circlets. There are 4 basals (BB), 5 infra-laterals (ILL), 5 laterals (LL), 4, 5, or 6 radials (RR), and 7 orals (OO). The plates are numbered clockwise around the theca from the left of the periproct. The positions of pectinirhombs on the theca may



TEXT-FIG. 20. Diagram of the morphology of a cryptorhomb.

be denoted by citing the two plates in which the half-rhombs are developed. Thus pectinirhomb L4:R3 has one half-rhomb in L4 and the other in R3. Pectinirhombs are only developed across certain sutures and some positions are occupied more frequently than others. No orals ever bear pectinirhombs and there is no marked preference for pectinirhombs to develop across sutures between different circlets (inter-circlet sutures) as opposed to sutures between plates of the same circlet (intra-circlet sutures).

C. THE MORPHOLOGY OF CRYPTORHOMBS

Cryptorhombs are rhombs composed of dichopores which open externally in pores (text-fig. 20). The term cryptorhomb is proposed because the entire length of the tangential part of all the dichopores is hidden from external view so that in many species the rhombs are inconspicuous.

The pores of cryptorhombs (text-figs. 3, 20) may be simple or sieve-like (compound pores of text-fig. 20). In almost all cases examined each dichopore opened in a sieve-pore at one end and a simple pore at the other. In all complete cryptorhombs one half-rhomb has sieve-pores only and the other has simple pores only. A few dichopores may

be reversed with respect to the others in some incomplete cryptorhombs. The dichotomous branching of the perpendicular canal which opens in a sieve-pore may proceed evenly in all branches to produce clusters of 2, 4, 8, 16, or 32 individual pores, or unevenly, producing intermediate numbers of individual pores. The individual pores may be circular, oval, or dumb-bell shaped: this depends on the stage of branching. Individual pores are usually surrounded by *pore rims* and may be set in shallow depressions or raised in rounded tubercles. Within a sieve-pore, individual pores may be arranged randomly or in rows. Simple pores may be developed on tubercles, or in or beside ridges on the plates. Nearly all simple pores have strongly developed rims.

Cryptorhomb dichopores (text-figs. 3, 20) resemble discrete dichopores of pectinirhombs in the sense that the inter-dichopore spaces are covered by unmodified thecal plate. Dichopores may be evenly developed throughout a cryptorhomb, which then has a regular rhombic outline and is *complete*. *Incomplete cryptorhombs* have few, irregularly spaced, dichopores and irregular outlines. Cryptorhomb dichopores may be weakly calcified within the theca.

Only one type of cryptorhomb (text-fig. 20), which corresponds in structure to a disjunct pectinirhomb with discrete dichopores, has been recognized. However, cryptorhombs may be complete or incomplete and the unusual rhombs of *Polycosmites* Jaekel may represent a second type of cryptorhomb, corresponding to multi-disjunct pectinirhombs in structure. Unfortunately no specimens are available.

Cryptorhombs are confined to and characteristic of the superfamily Hemicosmitida, members of which have thecae composed of a definite number of plates arranged in 3 or 4 circlets. These are designated by the same symbols as in the Glyptocystitida but the arrangement of plates is less constant. There may be 3 or 4 basals, 6 or 10 infra-laterals, 8 or 9 laterals, and, in the Hemicosmitidae, 9 radials. In the Caryocrinitidae the oral area is covered by a special 'tegmen' which apparently replaces the radial circlet. Cryptorhombs are not developed in tegminals but may be present in all other plates. In many species complete cryptorhombs are predominantly developed across inter-circlet sutures while incomplete cryptorhombs are confined to intra-circlet sutures of the lateral and infra-lateral circlets. There are thus rings of complete cryptorhombs which correspond to the inter-circlet sutures. Furthermore the arrangement of the pores of complete cryptorhombs is constant (text-fig. 21). In the BB:ILL ring sieve-pores occur in the basals; in the ILL:LL ring they are in the laterals; in the LL:RR ring (Hemicosmitidae only) they are in the radials. Incomplete cryptorhombs complicate this arrangement but functionally they are of minor importance.

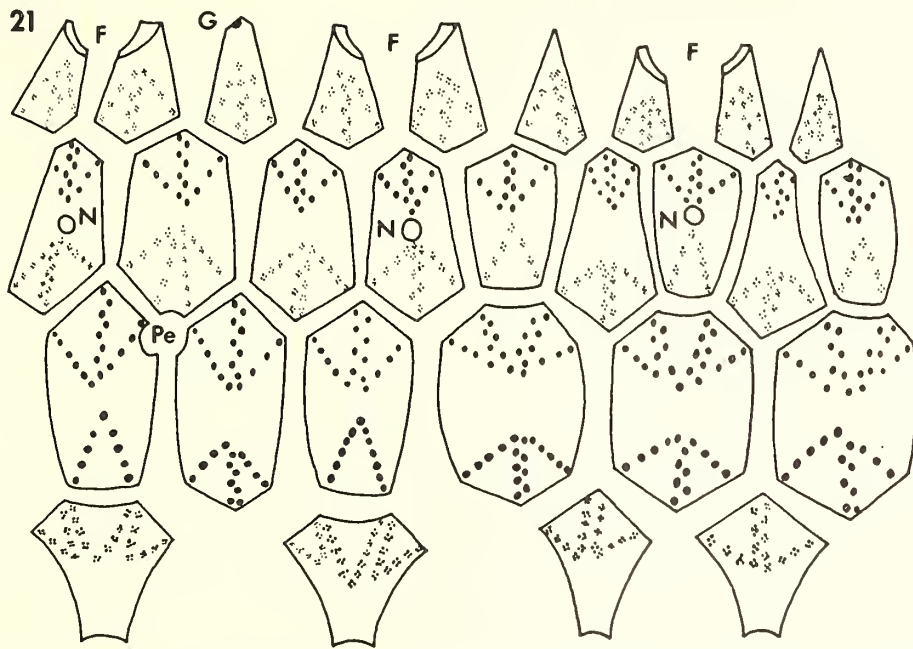
THE FUNCTION OF DICHOPORITE PORE-STRUCTURES

A. THE BASIS OF FUNCTIONAL INTERPRETATIONS

The principles on which this functional analysis of cystoid pore-structures has been based were outlined by Rudwick (1964*b*) but a brief résumé will now be given. It is necessary first to assume that any organ under investigation was functional and to suggest a function for it. This assumption may be tested in fossils only if it is possible to predict a structure which would serve the function efficiently and which is directly comparable with the preserved hard parts of the fossil. This prediction has been termed a *paradigm* by Rudwick (1960) and is assumed to have maximum efficiency within the

limits imposed by the materials of which the fossil structure is made. A close morphological similarity between the fossil structure and the paradigm would be expected if the former functioned efficiently. Where such similarity is found it is probable that the postulated function was served in life but this cannot be said to have been proved absolutely.

Three points arise in this connection. 1. The preserved hard parts of the fossil did not constitute the entire structure in life, i.e. at the time of functioning. It is necessary to reconstruct the unpreserved soft parts and in doing so it is assumed that the soft



TEXT-FIG. 21. Diagrammatic representation of the distribution of simple and sieve-pores in the theca of *Hemicosmites extraneus* Eichwald. Only complete cryptorhombs are shown. F, arm facet; G, gonopore; N, node in lateral plates; Pe, periproct. Based on RM. Ec5381.

(unpreserved) parts of the fossil bore the same relationship to the preserved hard parts that the soft parts of related living organisms do to their hard parts. For example, Sinclair's (1948, p. 306) suggestion that the dichopores of the pectinirhombs of *Glyptocystites* were lined with ciliated epithelium may be accepted since dichopores are invaginations of the external surface of the thecal wall and nearly all modern echinoderms have an external ciliated epithelium.

2. The second assumption that the fossil structure functioned efficiently is only a working assumption and may be modified to fit any case. To test any postulated function a close morphological similarity between the fossil structure and the paradigm is sought. If it is found, the fossil structure could have served the function efficiently. If not, it cannot be concluded that the structure did not serve the postulated function but only that it was inefficient if it did.

The early functional morphologists evolved as an empirical law the idea that any given organ is only developed to the minimum efficiency conducive with survival

(*minimum survival efficiency*) and not the maximum potential efficiency. A low relative efficiency in an organ may result from a low minimum survival efficiency, perhaps due to a lack of competition or low selective pressures. At present this is an hypothetical consideration since evaluation of minimum survival efficiencies in fossils is impossible and there is little information from living animals.

Any structure may form part of two (or more) functional systems, or may have two (or more) concomitant functions, each with different structural requirements. Such structures may become a compromise between the ideal cases. If it is possible to suggest the two (or more) functions, it may become possible to test whether departure from one paradigm is due to approximation to another.

A low relative efficiency in one structure may be compensated for by a high efficiency elsewhere in the system. Equally minimum survival efficiency may be achieved by a few efficient organs or a large number of less efficient organs. Thus the second assumption that the fossil structure functioned efficiently is only a working assumption and considerable information on the functioning of a fossil structure may be gained even when there is not a close comparison with the paradigm.

3. There is always a danger of using teleological language in functional analyses since 'function' and 'purpose' are sometimes used synonymously. Yet no fossil ever evolved a structure to serve a purpose. To investigate the 'effect' of a structure need neither imply function nor purpose. Thus if a chance rock fall produces a narrow crack between two boulders through which the tide washes, the crack will prevent particles of a diameter greater than its width from passing between the boulders. The crack may be analysed in the same way as zigzag slits in brachiopods (Rudwick 1964*a*) or pectinirhomb slits (p. 715) and will be found to have the same effect. Since it was a chance rock fall which produced the crack there can be no purpose behind it nor does it serve any function. Rudwick (1964*a*) concluded that if zigzag slits in brachiopods were protective they could have served this function efficiently. That is: the effect of zigzag slits in brachiopods was to reduce the maximum size of particles that could enter (or leave) the mantle cavity for any given gape. If fossil brachiopods behaved in a similar manner to living brachiopods, those with zigzag slits were better 'protected' from large particles than those without (for any given gape). This may have been beneficial to these brachiopods. The 'function' of a structure may be considered as a 'beneficial effect' or better still as the most beneficial of its several effects. Although the purpose of functional analyses is to determine the 'function' of structures, it is the mode of functioning, i.e. the sum of the 'effects' of the detailed morphology of the structures, which is investigated. In the next sections attempts are made to interpret the effects of the detailed morphology of pectinirhombs and cryptorhombs, having assumed that they were functional in life.

B. THE GENERAL FEATURES OF EXCHANGE SYSTEMS

Most authors have accepted a respiratory function for all cystoid pore-structures. It is true that Delpy (1942) has suggested that pectinirhombs and cryptorhombs were balancing organs and Hyman (1955) among others, has suggested that some canals may have been nutritive. However, Sinclair (1948, pp. 307-8) has shown how unlikely it is that pectinirhombs or cryptorhombs were balancing organs. If thecal canals were nutritive, they would be evenly distributed or at least present in all thecal plates. This is not always the case with pectinirhombs, cryptorhombs, and diplopores but apparently

it is the case with humatipores and humatirhombs. The most plausible function for pore-structures is respiration. If pore-structures were respiratory this was achieved by diffusion of oxygen and carbon dioxide and the pore-structures formed part of an exchange system. To test this hypothesis the paradigm of an exchange system must be examined.

The most essential feature of an exchange system is that only the 'exchange substance' or 'substances' should be exchanged; direct mixing must be prevented. There must be an *exchange surface* which allows the passage of the exchange substances while keeping the *donor* and *acceptor fluids* separate. In respiration the donor current for oxygen is also the acceptor current for carbon dioxide. Throughout donor current is used with reference to oxygen exchange. The rate of exchange will depend on the following factors:

1. *The area of the exchange surface.* The larger the area of the exchange surface, the greater the amount of exchange. The exchange surface should be as large as its strength will allow. Echinoderm skeletal calcite is a meshwork of calcite rods and soft tissue. Oxygen and carbon dioxide diffused not through the skeletal calcite but rather through the soft tissues. In echinoderms no more than half the area of an exchange surface was available for exchange because of this meshwork structure.

2. *The resistance to exchange of the exchange surface.* The resistance of an exchange surface will be proportional to its thickness and will depend on its nature. Although the walls of the thecal canals are heterogeneous only the soft tissue functioned as exchange surface. The thinner the walls are, the lower their resistance to exchange, and their strength, will be. The paramount function is to maintain separation between two fluids; rupture of the exchange surface could be fatal. The exchange surface may be as thin as is compatible with this stipulation.

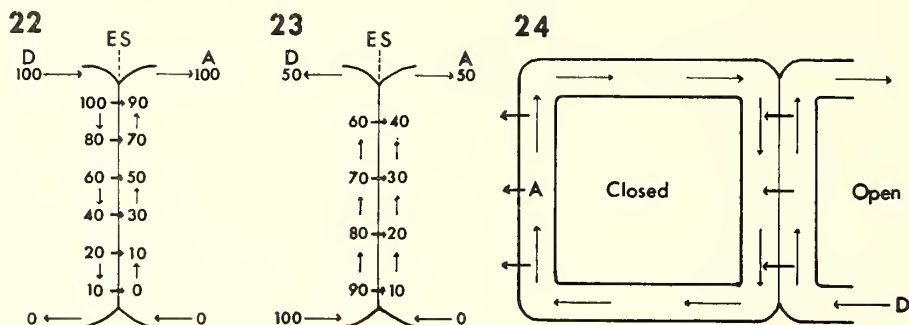
3. *The concentration gradient across the exchange surface.* No exchange will take place unless there is a gradient across the exchange surface, i.e. unless the concentrations of the exchange substances in the donor and acceptor fluids are different. In a static system the exchange substances would flow from higher concentrations to lower until the concentrations were equal when flow would cease. It is therefore necessary to have a current system to maintain the gradient. The most efficient system is a counter-current system (text-fig. 22). In a closed (internal) current system (text-fig. 24) an animal has control over the composition of the fluids circulating. In an open current system (text-fig. 24) however, devices to prevent recirculation of exhausted fluids and choking by extraneous particles are desirable.

Thus the paradigm of an exchange system will have a large area of exchange surface which is as thin as is compatible with its strength and a counter-current system (with provisions to prevent recirculation and choking where necessary). This paradigm will fit any exchange system such as a radiator (heat exchange), a kidney (urea excretion) or a gill (oxygen and carbon dioxide diffusion). It has not been developed purely for the present analysis.

C. DETAILED FUNCTIONAL INTERPRETATIONS

From a purely functional point of view there are two types of cystoid pore-structures: dichoporite and non-dichoporite. In dichoporite pore-structures the current which flowed through the thecal canals was the donor current (for oxygen) and formed part of an

open current system. The exchange surfaces were within the thecal cavity (endothecal) and protected from mechanical damage. In this section the detailed morphology of dichopore pore-structures (pectinirrhombs and cryptorhombs) will be compared with the paradigm of an exchange system and estimates of the relative efficiencies of the various types of rhomb made.



TEXT-FIGS. 22-4. Current and exchange systems.

22. A counter-current system. In the ideal case all the exchange substance is transferred from the donor to the acceptor current.

23. A system with both currents flowing in the same direction. The maximum potential exchange is 50%.

24. Diagram to illustrate closed and open current systems. In the donor current there is a potential danger of the entrance becoming choked with particles and of re-circulation from the exit.

A, acceptor current; D, donor current; ES, exchange surface. Figures represent concentrations of exchange substance; heavy arrows represent exchange; light arrows represent current directions.

1. *The area of the exchange surface.* An increase in the area of the exchange surface means an increase in the amount of exchange. In the simplest hypothetical case exchange



TEXT-FIG. 25. An isolated thecal plate of *Macrocytella mariae* Callaway to show external ridges which are effectively evaginations of the thecal wall.

would take place through the thecal wall. Oxygen requirements would be proportional to the volume, and rate of exchange to the surface area, of the theca. Throughout growth oxygen requirements would increase faster than the amount of exchange, thus limiting maximum size. Evaginations or invaginations of the thecal wall can counteract this effect without involving a change of gross thecal shape. Both are found in the Glyptocystitida. *Macrocytella* Callaway, the earliest known form, has externally ridged thecal plates (text-fig. 25). The ridges are formed by folds in the plates and are evaginations of the thecal wall. They increased the area, and also the strength, of the plates which are uniformly very thin (0.1 mm. in *M. mariae* Callaway). Exchange probably took place through the entire area of the thecal wall in *Macrocytella*.

Pectinirrhombs first appear in *Cheirocrinus* Eichwald, a direct descendent of *Macrocytella* (see Paul 1968). Dichopores are invaginations of the thecal wall which allow a differentiation of function between the thicker thecal plates (rarely if ever less than 0.5 mm.) and the thin dichopore walls (usually 0.01 mm.). Exchange was probably restricted

to the dichopore walls. These allow a large area for exchange within a small area of thecal surface. In *Cheirocrinus granulatus* (Jaekel) RM. Ec5384 (Pl. 135, figs. 3–5) one half-rhomb has a ratio of exchange area to thecal surface area of 7.84 : 1.

This ratio indicates the relative exchange efficiencies of different types of rhomb. In dichopore rhombs the closer the spacing of the dichopores and the greater their length and depth, the higher the ratio will be. Available measurements of spacing are summarized in Table 1. Dichopore width (W) would probably be given by $W = 2(h+1)$, where h = height of lining epithelial cells and 1 = length of cilia attached to the epithelial cells. At the limit of closeness of spacing the dichopores would be evenly spaced and the dichopore and inter-dichopore widths would be equal. This is the case in pectinirhombs with confluent dichopores and in complete cryptorhombs but not always in pectinirhombs with discrete dichopores nor in incomplete cryptorhombs. These latter were less efficient and tend to have higher values for spacing (Table 1).

Large pectinirhombs tend to have depressed outlines, a large number of dichopores, and to occur in large thecae. In any exchange system there is a distance within which all the exchange substance will be removed from the donor current as it flows along the exchange surface. This limits the length of a dichopore and the longest dichopores of both compressed and depressed pectinirhombs are about the same length (7–9 mm.). The exchange area of a pectinirhomb or cryptorhomb may be more efficiently increased by the addition of new dichopores than by the lengthening of existing dichopores. This may partly account for the tendency of large pectinirhombs to have depressed outlines (i.e. width greater than length). Maximum dichopore lengths in cryptorhombs are greater than those of pectinirhombs and oxygen exchange may have been less rapid in the former.

To summarize, the structure of dichopore rhombs compares closely with the paradigm of an exchange system as regards the area of the exchange surface. Pectinirhombs with confluent dichopores were relatively more efficient than those with discrete dichopores in terms of exchange area.

2. *The resistance to exchange of the exchange surface.* For maximum efficiency an exchange surface should be as thin as its strength will allow. Dichopore walls vary in thickness from less than 0.01 mm. up to 0.03 mm. in rare cases, whereas the thecal wall is 0.1 mm. thick in *Macrocystella mariae* Callaway, rarely, if ever, less than 0.5 mm. in *Cheirocrinus* and many Glyptocystitida have thecal walls 2–3 mm. thick. Dichopore walls are very much thinner than other skeletal elements and pectinirhombs were potentially weak areas of the theca. The morphology of dichopores, as thin tubes or isoclinal folds, allows great strength and rigidity for a thin surface. It also allows a large surface area without increasing the volume of the theca and thus satisfies both this and the previous requirements.

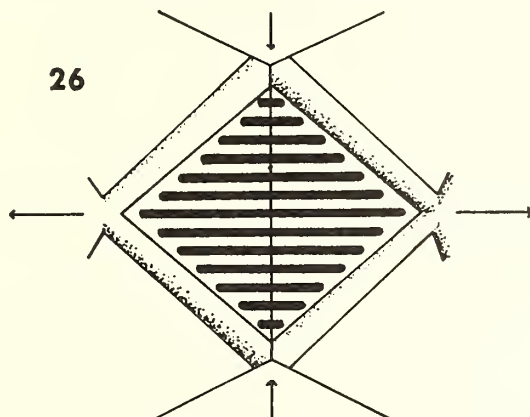
Pectinirhombs with conjunct slits were particularly susceptible to fracture or distortion by forces acting on the surface of the theca. It was essential to maintain rigidity for normal functioning and this could be achieved by solid ridges in the positions shown in text-fig. 26. Such ridges impart both strength and rigidity. Ridges are found in the positions suggested in some cystoids with conjunct pectinirhombs. In species of *Cheirocrinus* with discrete dichopores the ridges are often incorporated in the plate 'ornament' of radiating ridges. These ridges strengthened the plates in general and may only

TABLE 1. Spacing of Dichopores in Pectinirrhombs. The values for spacing are determined by measuring 10 dichopores and 10 inter-dichopore spaces and expressing the average as 1 slit per 0. xxx mm. In pectinirrhombs with fewer than 10 dichopores the average was based on the maximum number of dichopores measurable. The averages for each type of pectinirrhomb are based on the total number of measurements (No.)

	Species	Average	Spacing Range	No. of measurements
A. Conjunct pectinirhombs with discrete dichopores				
	<i>Cheirocrinus</i> sp.	0.316	0.217-0.415	2
	<i>C. giganteus</i> Leuchtenberg	0.273	..	1
	<i>C. granulatus</i> (Jaekel)	0.253	..	1
	<i>C. cf. atavus</i> (Jaekel)	0.106	..	1
	<i>C. languedocianus</i> Thorai	0.370	0.350-0.390	4
B. Conjunct pectinirhombs with confluent dichopores				
	<i>Homocystites alter</i> Barrande	0.215	0.205-0.225	2
	<i>H. constrictus</i> (Bather)	0.2025	0.201-0.204	2
	<i>Pleurocystites elegans</i> Billings.	0.196	..	1
	<i>P. filitextus</i> Billings	0.241	..	1
	<i>P. cf. rugeri</i> Salter	0.20 approx.	..	1
	<i>P. squamosus</i> Billings	0.171	..	1
C. Disjunct pectinirhombs with discrete dichopores				
	<i>Cheirocrinus</i> sp.	0.174	..	1
	<i>C. anatiformis</i> (Hall)	0.257	0.25-0.27	4
	<i>C. forbesi</i> Billings	0.273	0.25-0.29	6
	<i>Echinoencrinites angulosus</i> Pander	0.27	0.21-0.31	3
	<i>E. senckenbergii</i> von Meyer	0.33	0.32-0.34	3
	<i>E. reticulatus</i> Jaekel	0.427	0.41-0.44	3
	<i>Erinocystis</i> sp.	0.38	..	1
D. <i>Glyptocystites</i> type				
	<i>Glyptocystites ehlersi</i> Kesling	0.197	0.19-0.20	3
	<i>G. multiporus</i> Billings	0.193	0.18-0.20	10
	<i>G. regnelli</i> Sinclair	0.206	0.20-0.22	5
	<i>G. batheri</i> Sinclair	0.225	0.205-0.245	7
E. Disjunct pectinirhombs with confluent dichopores				
	<i>Sphaerocystites multifasciatus</i> Hall	0.223	0.212-0.225	4
	<i>Jaekelocystis hartleyi</i> Schuchert	0.168	0.150-0.180	4
	<i>Lepadocystis moorei</i> (Meek)	0.169	0.165-0.175	6
	<i>Apiocystites pentrematoides</i> Forbes	0.208	0.200-0.214	3
	<i>Strobilocystites calvini</i> White	0.276	0.265-0.285	6
	<i>Lovenicystis angelini</i> (Haeckel)	0.218	0.201-0.236	2
	<i>Lipsanocystis traversensis</i>	0.152	0.151-0.154	14
	Ehlers and Leighley			
	<i>Tetracystis oblongus</i> (Forbes)	0.156	0.153-0.159	3
	<i>Lepocrinites gebhardii</i> Conrad	0.250	..	2
	<i>Pseudocrinites gordonii</i> Schuchert	0.167	0.160-0.174	6
	<i>P. bifasciatus</i> Pearce	0.177	0.168-0.187	3
	<i>P. pyriformis</i> Paul	0.257	0.233-0.272	3
	<i>Staurocystis quadrifasciatus</i> (Pearce)	0.193	0.190-0.201	6
	<i>Glansicystis baccata</i> (Forbes)	0.205	0.190-0.220	6
		Over-all averages	Range	No.
Type A		0.306	0.106-0.415	9
B		0.205	0.171-0.241	8
C		0.300	0.174-0.440	21
D		0.205	0.193-0.245	25
E		0.192	0.151-0.285	68

incidentally have strengthened the pectinirhombs. In *Homocystites constrictus* (Bather) (Pl. 134, fig. 5) and *Pleurocystites* spp. (Pl. 134, figs. 7, 8) rims occur which are independent of the plate ridges and whose strengthening effect was confined to the area immediately adjacent to the pectinirhombs.

In fully developed disjunct pectinirhombs the intra-rhomb areas between the slits would resist forces acting on the thecal surface. In disjunct pectinirhombs with discrete dichopores the intra-rhomb areas tend to be large (Pl. 135, figs. 1, 9) and this partly restores the strength of the rhomb-bearing plates. In cryptorhombs (Pl. 138, fig. 4; Pl. 139, fig. 1), with only rows of pores, this restoration is virtually complete. In disjunct pectinirhombs with confluent dichopores the intra-rhomb areas tend to be smaller but the



TEXT-FIG. 26. A conjunct pectinirhomb with ridges which deflect forces acting within the plate and impart rigidity to the pectinirhomb.

adsutural portions of the vestibule rims develop within them (Pl. 136, fig. 3; Pl. 137, fig. 1). During growth of a disjunct pectinirhomb some marginal slits were conjunct and subject to the same weakness as conjunct pectinirhombs. In disjunct pectinirhombs with confluent dichopores the adsutural portions of vestibule rims arise early in development in exactly the position postulated to strengthen conjunct pectinirhombs (Pl. 137, fig. 1). No such rims are present in disjunct pectinirhombs with discrete dichopores.

Uncalcified dichopores would allow a greater exchange area than calcified dichopores since only the soft tissues function as exchange surface. In pectinirhombs distortion or disarticulation would probably occur if the dichopores were uncalcified but in cryptorhombs strength is provided by the covering of thecal plate. It is still essential to have rigid dichopore walls to prevent the dichopores themselves from distorting (under pressure differences or due to gravity) since this would interrupt the functioning of the cryptorhomb. A maximum movement of only 0.05 mm. by two adjacent dichopore walls would completely close a dichopore or inter-dichopore space. Calcification of dichopores imparts rigidity at the expense of the available area of exchange.

Most pectinirhombs and cryptorhombs have strengthening structures closely associated with them indicating they were areas of weakness. The conclusion that this weakness was mainly due to the dichopore walls seems inescapable. Dichopore walls were not

only thin absolutely but relatively so thin that the limits of their strength were reached and strengthening devices became necessary to counteract this weakness. In this respect dichoporite pore-structures agree closely with the paradigm of an exchange system. Further conclusions are that conjunct pectinirhombs were intrinsically weaker than disjunct pectinirhombs and all pectinirhombs were weaker than cryptorhombs. Strengthening devices in pectinirhombs with confluent dichopores apparently allowed a weaker structure with a better exchange area to thecal surface area ratio. Disjunct pectinirhombs with confluent dichopores were strengthened throughout a longer period of their growth than those with discrete dichopores.

3. *Protective devices and devices to prevent recirculation.* The currents which flowed within dichopores formed part of an open current system. Therefore devices to prevent choking by extraneous particles and recirculation of deoxygenated sea-water would have been beneficial to exchange. Such devices are also very useful in determining current directions since they indicate which pores were entrances and which exits. Clearly it is more efficient to modify the entrance (rather than the exit) with a protective device since this will prevent entry of harmful particles. Equally, exhausted sea-water in the vicinity of the entrance will be sucked in by the in-current. Recirculation can only be prevented by modifying the exit to direct the out-current away from the entrance and into the ambient sea-water for remixing. Protective devices, which will be considered first, indicate entrances and devices to prevent recirculation indicate exits.

A protective device is a structure which reduces the maximum size of particles that may pass through an aperture without interfering with the functioning of the aperture. There are only three classes of structure which fulfil these requirements: meshes, grilles, and narrow slits. Paradigms for all three have been defined by Rudwick (1961, meshes and grilles; 1964a, slits). The maximum particle which can pass through the device is termed the critical particle and is of critical diameter. In an ideal protective device the critical diameter is the same at all points within the aperture.

Two types of harmful particle may be recognized. *Passive particles* are any particles in suspension (animal or plant debris, sediment, etc.) which may choke the dichopores but not attack the cystoid. *Active particles* are organisms which may attack the cystoid

EXPLANATION OF PLATE 134

Stereophotos of conjunct pectinirhombs

A. with discrete dichopores.

Fig. 1. *Cheirocrinus giganteus* Leuchtenberg. BMNH E16130, basal rhombs.

Figs. 2, 4 *Cheirocrinus* sp. SM A3138 (fig. 4), SM A3139 (fig. 2). External moulds of isolated plates.

Fig. 3. *Cheirocrinus granulatus* (Jaekel). RM Ec5384.

Fig. 9. *Cheirocrinus languedocianus* Thor. Ubahgs coll. latex impression showing incomplete pectinirhombs and demirhombs in radial and lateral plates.

B. with confluent dichopores.

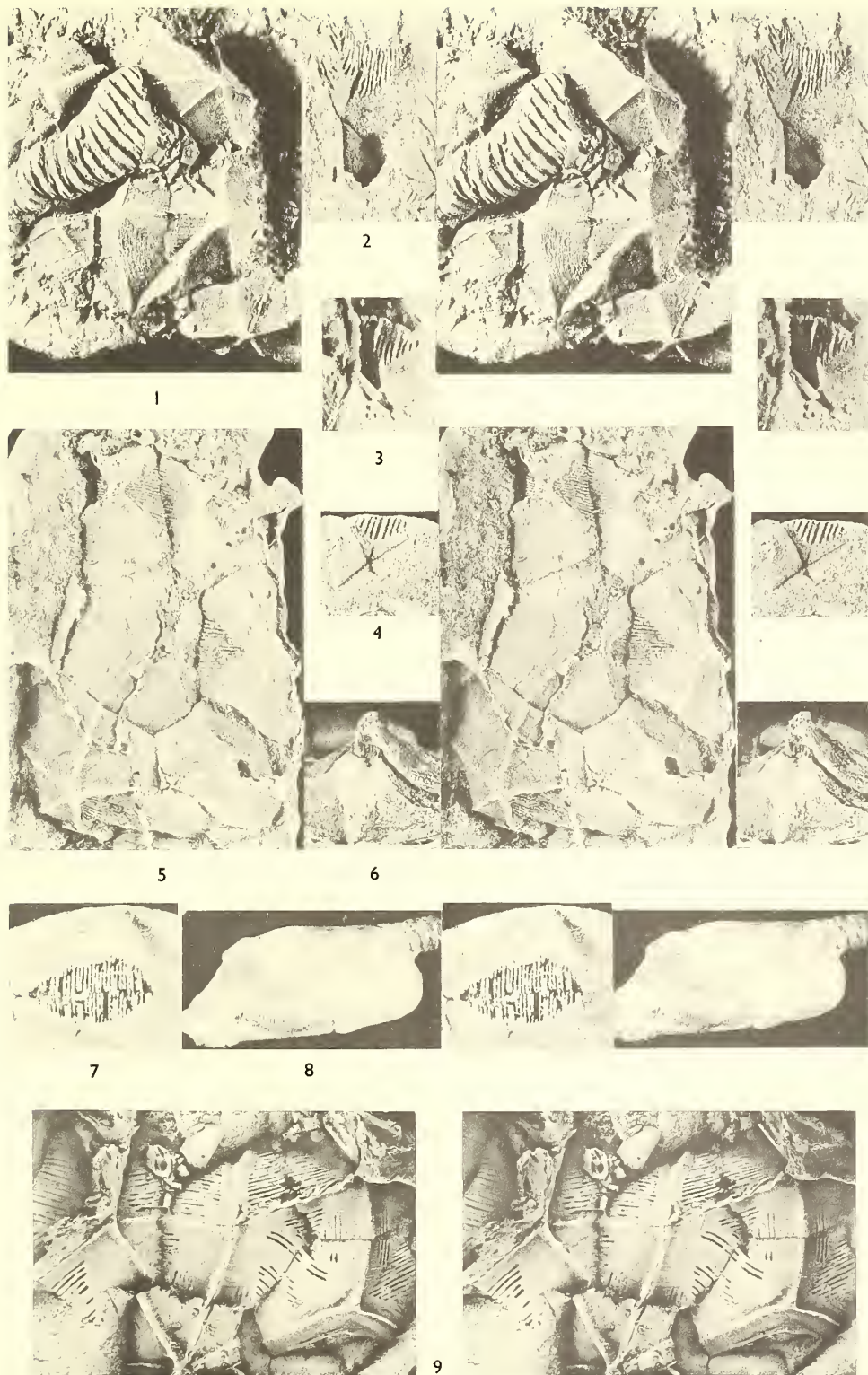
Fig. 5. *Homocystites constrictus* (Bather). HM 3541a, latex impression showing rhombs B2:IL2, L1:L2, and R1:R2. Note the rim on L2 (middle rhomb).

Fig. 6. *Pleurocystites rugeri* Salter. LU 3175, latex impression of L3:L4.

Fig. 7. *Pleurocystites elegans* Billings. SM A53059. L3:L4.

Fig. 8. *Pleurocystites filitextus* Billings. BMNH E16047. L4:L3.

Figs. 1, 8, 9 $\times 2$, figs. 2-7 $\times 3$. All whitened with ammonium chloride sublimate.



PAUL, Cystoid pore structures

by boring into it, attaching to it or browsing off cilia, etc. Dichopores may be regarded as long thin tubes whose critical diameter at any given point is the minimum width. Complete protection against passive particles may be achieved if the critical diameter of the entrance is less than that of any other point along the tube. Any spherical particle capable of entering the tube will pass right through without becoming lodged. Complete protection against active particles, which may be able to swim against currents, can only be achieved if the critical diameters of both the entrance and the exit are less than the diameter of the smallest active particle. As nothing is known about

TABLE 2. Ratios of slit lengths and areas in disjunct pectinirhombs

Species	Rhomb	Ratios	
		$\frac{\text{Lengths longer slit}}{\text{shorter slit}}$	$\frac{\text{Areas longer slit}}{\text{shorter slit}}$
A. Discrete dichopores			
<i>Echinoecrinites angulosus</i> BMNH E29102	B2:1L1	1.27 (7)	0.82 (5)
	B2:1L2	1.21 (11)	0.84 (11)
<i>E. reticulatus</i> RM Ec5515	B2:1L1	1.25 (6)	0.94 (6)
	B2:1L2	1.27 (8)	1.31 (8)
	L4:R3	1.11 (9)	0.94 (9)
<i>E. senckenbergii</i> BMNH E29095	B2:1L1	1.54 (8)	0.97 (8)
	B2:1L2	1.43 (6)	1.06 (6)
	L4:R3	1.16 (10)	0.87 (10)
<i>Cheirocrinus anatiformis</i>	R2:R3	1.14 (15)	1.08 (15)
B. Confluent dichopores			
<i>Glyptocystites multiporus</i>	L1:L2	1.46 (9)	1.46 (9)
<i>Staurocystis quadrifasciatus</i>	L1:R5	1.37 (18)	0.97 (18)
<i>Lovenicystis angelini</i> RM Ec5053	L1:R5	1.77 (13)	1.38 (13)
RM Ec5066	L1:R5	1.30 (17)	0.98 (17)
<i>Glauiscystis baccata</i> Bu Ho55	L1:R5	1.15 (9)	1.09 (9)
	L4:R3	1.43 (9)	1.19 (9)
GSM 7380	L1:R5	2.63 (8)	1.91 (8)

Figures in brackets represent the number of measurements upon which each ratio was based.

active particles it is impossible to investigate protection against them. Only passive particles are considered below.

The dichopores of pectinirhombs open as slits and if protected the entrances should form protective slits. In conjunct pectinirhombs each slit runs the entire length of the dichopore and acts as both entrance and exit. In *Cheirocrinus ?atavus* (Jaekel) BMNH E23515 and *Pleurocystites filitextus* Billings BMNH E7600b (Pl. 140, fig. 2) slit widths are slightly less than dichopore widths within the theca. In these cases the slits were protective.

In disjunct pectinirhombs the slits of the two half-rhombs were of different lengths. In many cases the longer slits are also narrower. To satisfy the requirements of a protective device the critical diameter of the incurrent slit must be reduced without reducing current flow. If protection is achieved by reducing the width, constant current velocity may be maintained by a corresponding increase in slit length since the velocity is inversely proportional to the cross-sectional area of the slit. In the ideal case the ratio of entrance to exit slit length will be greater than unity but the ratio of the areas will equal unity. Available measurements are shown in Table 2. In cases where the longer

slits were also narrower they could have been protective. In cases where the slit widths are equal they could still have been protective if both were narrower than the dichopore width within the theca.

The pectinirhombs of *Lipsanocystis magnus* Stumm (Pl. 140, fig. 4) show microscopic bars across the slits of both half-rhombs. These bars reduce the critical diameter of both apertures. Preservation is not quite adequate to determine which slits are better protected or if any difference exists. The formation of these microscopic grilles may be unique to *L. magnus*; perhaps a response to its muddy environment or to active particles since both apertures are modified. Alternatively it may be that the preservation of most glyptocystitids is not adequate for these delicate structures to be detectable. In the latter case the arguments for protective devices in pectinirhombs may need some modification.

TABLE 3. Critical diameters in pectinirhombs and cryptorhombs

Rhomb type	Entrance			Exit		
	Average	Range	No.	Average	Range	No.
Pectinirhombs						
conjunct discrete	0.115	0.02-0.19	6	..	..	..
conjunct confluent	0.066	0.05-0.08	8	..	..	..
disjunct discrete	0.113	0.05-0.18	10	0.162	0.12-0.20	8
confluent disjunct	0.075	0.07-0.095	5	0.104	0.09-0.012	5
Cryptorhombs	0.058	0.04-0.07	13	0.20	0.10-0.35	13

No. = Number of rhombs of each type measured. In pectinirhombs with variable slit widths the average width of all slits was calculated.

In cryptorhombs the dichopores open as pores, at least one of which is sieve-like, being composed of a cluster of fine pores. If sieve-pores were protective they formed protective meshes. Measurements given in Table 3 show that the critical diameters of sieve-pores are much less than those of simple pores. The areas (Table 4) of simple and sieve-pores are often approximately equal however. Again protection could be provided while interfering to the least extent possible with current flow.

Particles prevented from entering dichopores by protective devices would choke the slits and pores themselves unless removed. Clearance could be achieved by surface ciliary currents, the particles being carried in the same direction as the currents within the

EXPLANATION OF PLATE 135

Stereophotos of disjunct pectinirhombs

A. with discrete dichopores.

- Fig. 1. *Cheirocrinus* sp. nov. SM A15966. Latex impression of isolated plate.
- Figs. 2-5. *Cheirocrinus granulatus* (Jaekel). RM Ec5384. Fig. 2, internal surface of basal plate; figs. 3-5, views of isolated half-rhomb to show relationship between dichopores and slits.
- Fig. 6. *Cheirocrinus* sp. BMNH E15983.
- Fig. 7. *Echinoencrinites senckenbergii* von Meyer. BMNH E29102, rhombs B2:IL1 and B2:IL2.
- Fig. 8. *Echinoencrinites reticulatus* Jaekel. BMNH E29095. B2:IL1 and B2:IL2.
- Figs. 9, 12. *Cheirocrinus anatifformis* (Hall). GSC. B2:IL2 (fig. 9) and radials (fig. 12).
- Fig. 10. *Echinoencrinites reticulatus* Jaekel. RM Ec5515. B2:IL1.

B. with confluent dichopores.

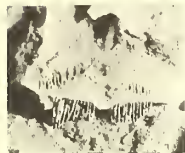
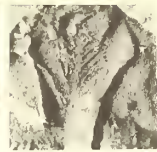
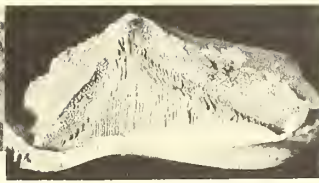
- Fig. 11. *Glyptocystites multiporus* Billings. GSC 1387g (Lectotype). B2:IL1, B2:IL2, and R1:R2. Note the adsutural rim on R2 (large upper rhomb).
- Figs. 1, 6-9, 11, 12 × 2, figs. 2-5, × 3, fig. 10, × 5. All whitened with ammonium chloride sublimate.



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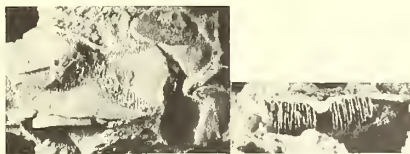
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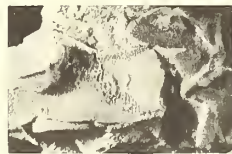
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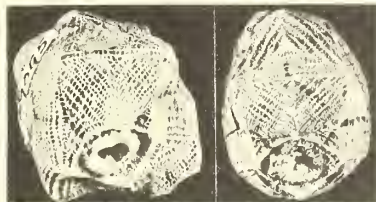
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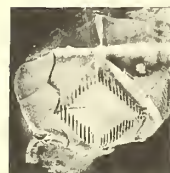
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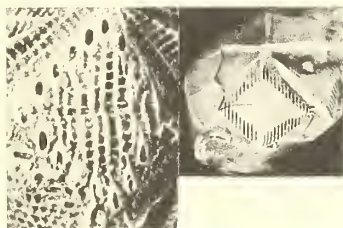
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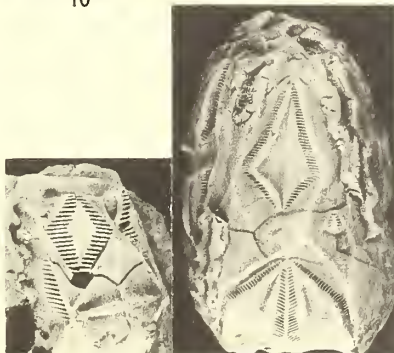
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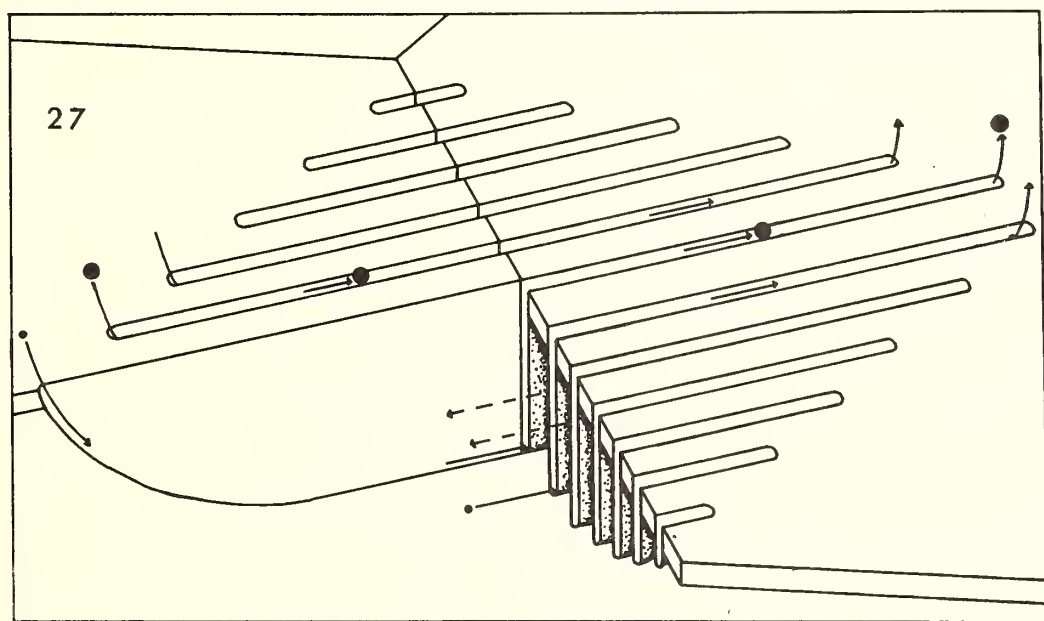


TABLE 4. Areas of simple and sieve-pores in cryptorhombs

Specimen	Area of sieve-pore (entrance)	Area of simple pore (exit)
<i>Hemicosmites</i> sp. RM Ec5364	0.0707 sq. mm.	0.0471 sq. mm.
<i>H. extraneus</i> RM Ec5283	0.0226	0.0201
<i>H. sp. nov.</i> RM Ec2280	0.0154 (radials) 0.0502 (laterals)	0.0314–0.0572
<i>H. cf. verrusosus</i> BMNH E15994	0.0491	0.0433 0.0201–
<i>H. malum</i> RM Ec5517	0.0201 (basals) 0.0402 (laterals)	0.0254
<i>H. cf. pyriformis</i> BMNH E7592	0.0314	0.0227
<i>Caryocrinites ornatus</i> SM A50958*	0.0308	0.0154
<i>C. roemeri</i> BMNH E29105*	0.0628	0.0628
<i>C. septentrionalis</i> RM Ec25493	0.0226	0.0314
<i>Thomacystis tuberculata</i> BMNH E16300	0.0176	0.0176

Unless otherwise stated the area of sieve-pores was taken from lateral plates; all areas of simple pores are from infra-lateral plates.

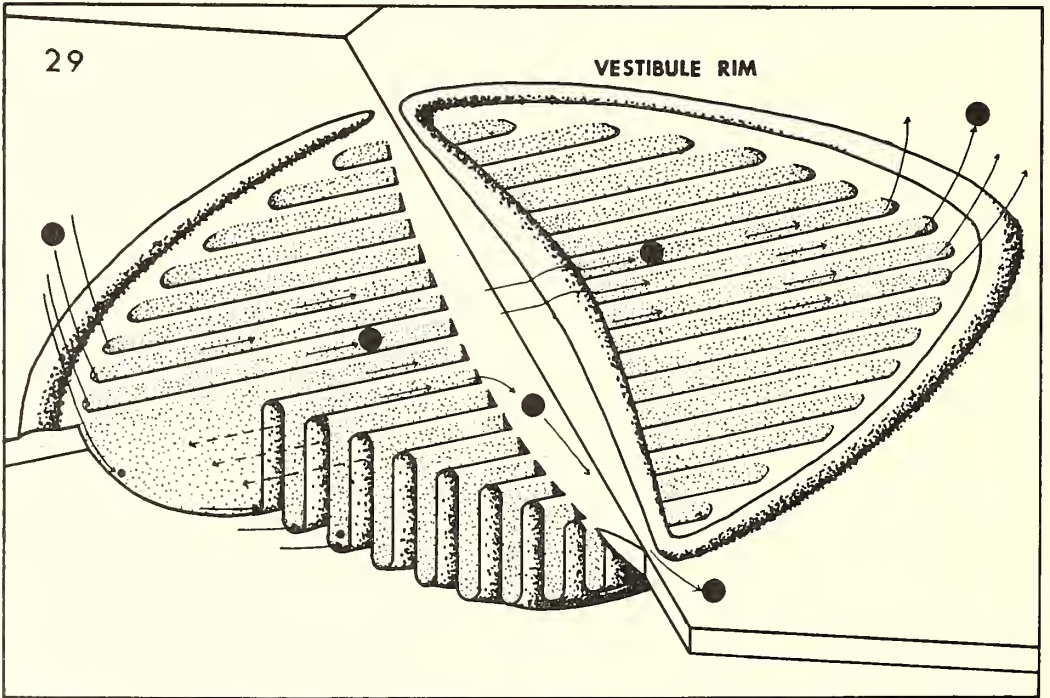
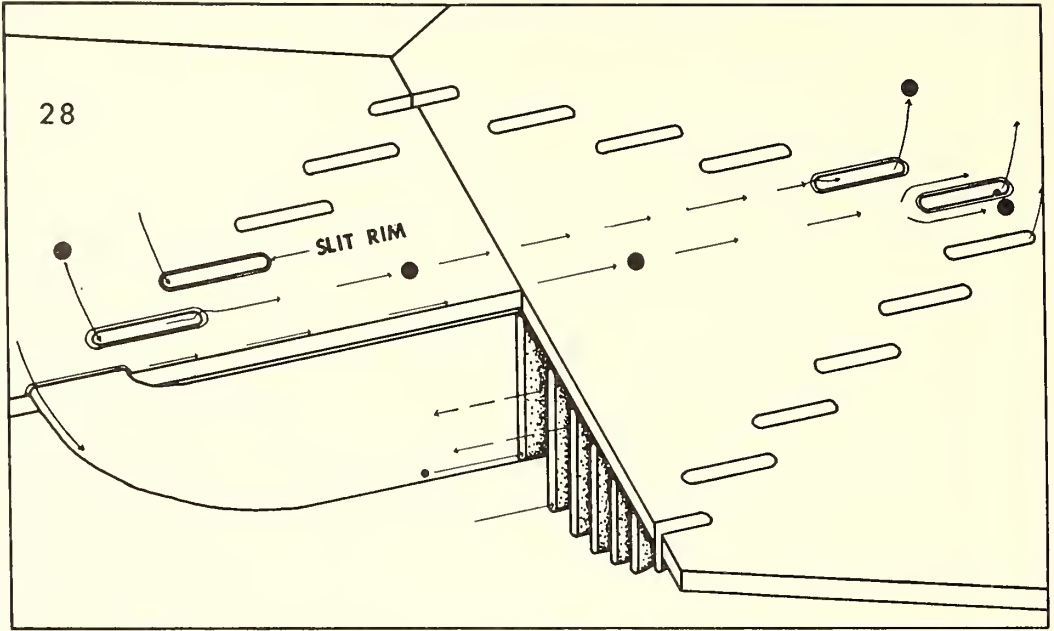
* These specimens have sieve-pores at both ends of dichopores in complete cryptorhombs. However, there are fewer larger pores per cluster where one would normally expect simple pores.



TEXT-FIG. 27. Supposed paths of extraneous particles in conjunct pectinirhombs. Solid arrows indicate external currents; dashed arrows internal currents.

dichopores. In conjunct pectinirhombs particles strained from the in-current would be passed along the slit until they reached the out-current and would then be carried away from the theca (text-fig. 27). Similar currents could have been present in disjunct pectinirhombs and cryptorhombs but the slit, vestibule, and pore rims would render them less effective (text-figs. 28, 29).

We may conclude that the narrower slits of disjunct pectinirhombs and the sieve-pores of cryptorhombs reduced the critical diameters of these apertures, which were



TEXT-FIGS. 28, 29. Possible paths of extraneous particles in disjunct pectinirhombs. Note that the slit and vestibule rims make it more difficult for the excurrent to remove the particles.

therefore entrances. Absolute critical diameters shown in Table 3 indicate that cryptorhombs were better protected than pectinirhombs. However the latter, particularly conjunct pectinirhombs, were better able to prevent the protective devices themselves from becoming choked. This may account for the occurrence of conjunct pectinirhombs in all but one rhomb-bearing member of the Pleurocystitidae. Members of this family were probably vagrant with the theca resting on the substrate (Paul 1967c) and may have encountered many more particles than more typically pelmatozoan cystoids.

For maximum efficiency devices to prevent recirculation of exhausted sea-water must do so while interfering with current flow to the least possible extent. The most fundamental requirement is to have two apertures and to keep them apart. How far apart will depend on the volume, velocity, and direction of the out-current. Even if the entrances were capable of detecting oxygen-depleted water they could not prevent it from entering without arresting or reversing the currents. Recirculation can only be prevented effectively by modifying the exit to direct the out-current away from the entrance.

Recirculation may occur within a single rhomb or from one rhomb into another. In a theca with many rhombs recirculation of the second type may be prevented by grouping exits together. In general where two or more apertures are found within a single plate they are either exits or entrances (text-figs. 30, 31). Recirculation within a single rhomb may be prevented by mechanical barriers or by devices to project the out-current through the boundary layer into the ambient sea-water for remixing. The *boundary layer* is the layer of fluid immediately adjacent to the surface of an immersed solid, within which viscosity is the most important single force controlling flow. Cilia beat within the boundary layer and without them water in contact with the external surface of an echinoderm would remain unchanged in all but the most turbulent seas. Water emerging from the dichopores would be recirculated by surface cilia unless forced through this layer. Mechanical barriers between the entrance and exit were therefore probably less efficient than were devices to project the out-current through the boundary layer.

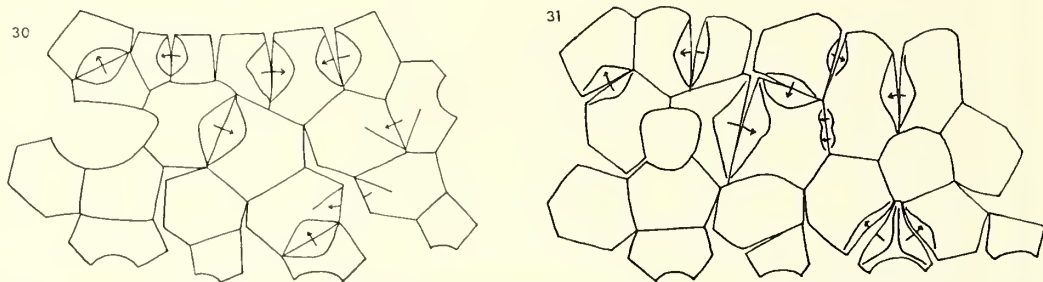
The best method to determine the effects of such structures is to construct models and test them under simulated conditions as close as possible to those under which they operated in life (cf. Rudwick 1961, Jefferies and Minton 1965). Time has not been available to do this and the conclusions outlined below are tentative.

The conjunct pectinirhombs of *Homocystites constrictus* (Bather) (Pl. 134, fig. 5) have distinct rims on one half-rhomb only. Water passing along the dichopores towards these rims would be deflected away from the theca. Where two half-rhombs are developed in a single plate they are either rimmed or unrimmed. Current directions shown in text-fig. 30 are derived from the presence of these rims.

Sinclair (1948) suggested that the adsutural ridges on one half-rhomb of each pectinirhomb in *Glyptocystites* spp. were mechanical barriers to recirculation. This suggestion seems likely although as yet without practical confirmation. Again where two or more half-rhombs occur in one plate they are either with or without ridges. In text-fig. 31 the arrows point to the plates with ridges.

Disjunct pectinirhombs with confluent dichopores have a closed vestibule rim on one half-rhomb and an open rim on the other. The adsutural portion of the closed rim would have directed the out-current away from the theca. The adsutural portion would have acted as a mechanical barrier to recirculation as Sinclair suggested for the pectinirhombs of *Glyptocystites*. In addition the closed vestibule rims united all the currents of the

constituent dichopores and probably reinforced them. If out-currents they would have passed through the boundary layer more readily. The pectinirrhombs of *Jaekelocystis hartleyi* Schuchert (Pl. 137, figs. 7, 9, 10) have closed vestibule rims which form a pore 0.5 mm. in diameter. This pore would considerably increase the velocity of currents passing through it. In disjunct pectinirrhombs with a constant slit width in both half-rhombs, the shorter slits would have had faster currents. Fast in-currents would be more likely to suck in extraneous particles but fast out-currents would be more likely to pass through the boundary layer and disperse. Shorter slits and closed vestibule rims therefore probably indicate exits.



TEXT-FIGS. 30, 31. Current patterns in *Cheirocrinus* and *Glyptocystites*.

30. Diagram to show the arrangement of thecal plates and pectinirrhombs in *Cheirocrinus anatiformis* (Hall).

31. Diagram to show the arrangement of thecal plates and pectinirrhombs in *Glyptocystites ehlersi* Kesling.

Arrows indicate supposed current directions in the pectinirrhombs. Note where more than one half-rhomb is developed within a single plate they are usually of the same type (i.e. either entrance or exit). Plate outlines based on Kesling 1962 (text-fig. 30) and 1961 (text-fig. 31).

Many cryptorhombs have simple pores developed beside or within ridges on the plate surface. These ridges could have directed currents away from the theca. In *Caryocrinites septentrionalis* Regnéll (Pl. 139, fig. 5) the ridges beside simple pores are more strongly developed than those associated with sieve-pores. In *Hemicosmites* spp. (Pl. 138, figs. 1, 5) simple pores are developed into chimney-like tubercles and may be interpreted as chimneys. The further away from the thecal surface the out-current emerges the less likely it is to be recirculated by surface ciliary currents. These were therefore probably exits.

EXPLANATION OF PLATE 136

Stereophotos of disjunct pectinirrhombs with confluent dichopores

Figs. 1, 7. *Pseudocrinites gordonii* Schuchert. BMNH E23122. L1:R5 (fig. 1) and B2:IL2 (fig. 7). Note the vestibule rims typical of this type of pectinirrhomb.

Fig. 2. *Callocystites jewetti* Hall. GSC 14686. L4:R3.

Fig. 3. *Pseudocrinites pyriformis* Paul. BU Ho10. L1:R5.

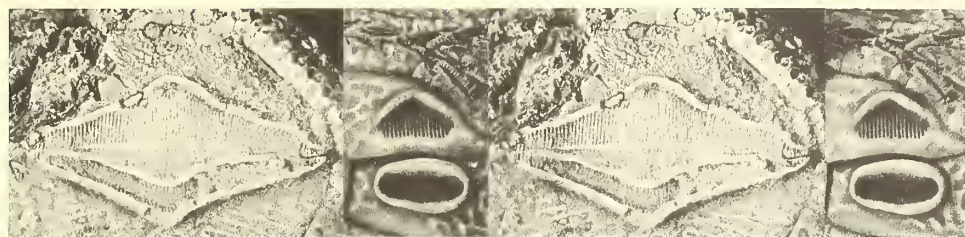
Figs. 4, 5. *Lovenicystis angelini* (Jaekel). RM Ec5066. L4:R3 (fig. 4) and L1:R5 (fig. 5).

Fig. 6. *Strobilocystites calvini* White. UI. L4:R3.

Fig. 8. *Sphaerocystites multifasciata* Hall. BMNH 22960. B2:IL2.

Fig. 9. *Pseudocrinites perdewi* Schuchert. USNM 35072. L4:R3.

Figs. 1, 3-5, 7, 8 $\times 3$, figs. 2, 6, 9 $\times 2$. All whitened with ammonium chloride sublimate.



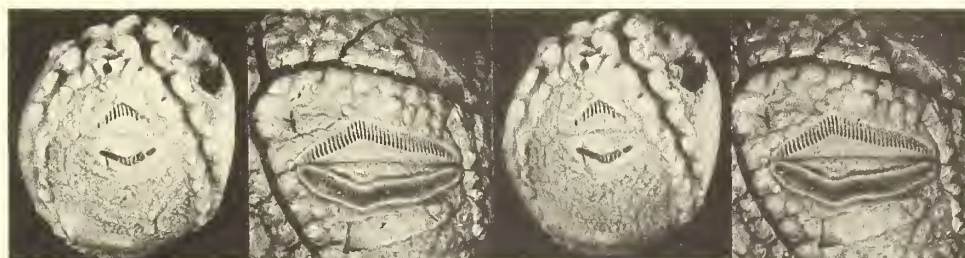
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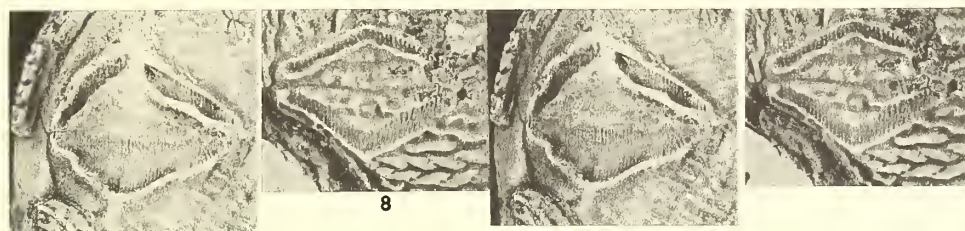
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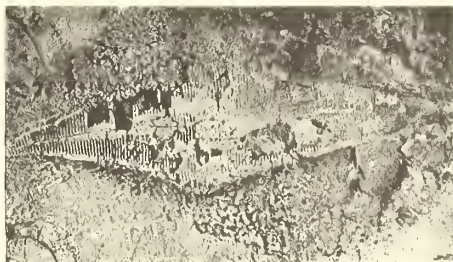


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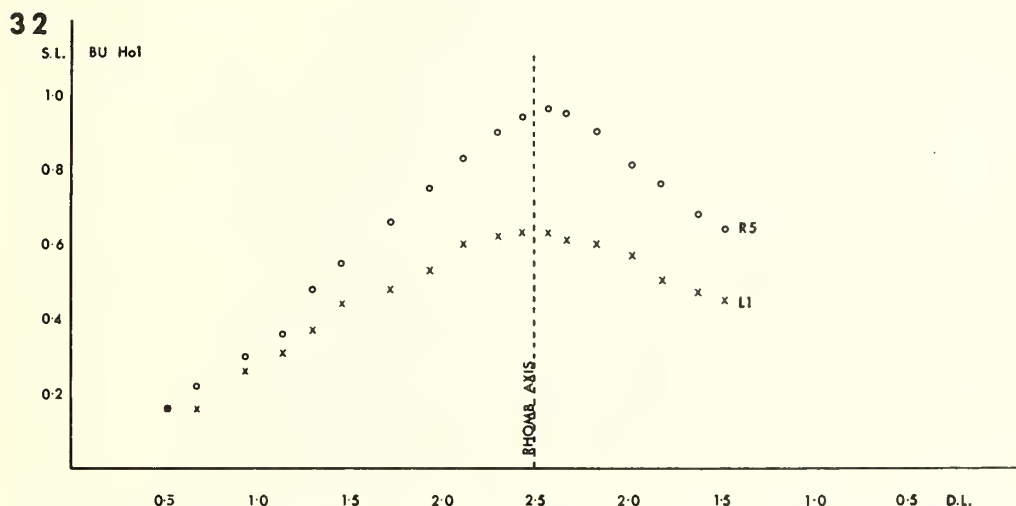


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To conclude, devices which prevented recirculation are apparently present in most cryptorhombs and disjunct pectinirhombs but are generally absent from conjunct pectinirhombs. Suggested entrances were described under protective devices and exits under devices to prevent recirculation. In all cases these interpretations should be, and in fact are, complementary. Thus in disjunct pectinirhombs longer slits were interpreted as entrances and shorter slits as exits. In cryptorhombs sieve-pores were interpreted as entrances and simple pores as exits. Closed vestibule rims in pectinirhombs were interpreted as being associated with exits and they always occur on the half-rhombs with shorter slits. All these interpretations confirm each other and also confirm the presence and direction of donor currents within dichopore pore-structures.

4. *The maintenance of a concentration gradient.* A counter-current system is the most efficient method of maintaining a concentration gradient. Ciliary currents within the dichopores would be expected on *a priori* grounds as suggested by Sinclair (1948). The viscous effect of the boundary layer would be even more marked in a restricted space such as a dichopore. No matter how turbulent the seas, water within the dichopores would not be disturbed without cilia.



TEXT-FIG. 32. Graph to show relationship between slit length and dichopore length in pectinirhomb L1:R5 of *Staurocystis quadrifasciatus* (Pearce), BU Ho l. Lower scale reversed about the rhomb axis for clarity. Note that the slit lengths are proportional to the dichopore lengths and the slit lengths in L1 are constantly less than those of R5.

If currents were present, sea-water flowed within the dichopores forming the donor current which was part of an open current system. The best evidence for the presence and direction of the donor current has been outlined in the preceding section. Additional evidence is found in the relationship between slit and dichopore lengths in pectinirhombs and between pore counts and dichopore length in cryptorhombs. Adaxial dichopores are longer and deeper than marginal dichopores. If the current velocity were constant in all dichopores more water would pass through the larger dichopores per unit time. The capacity of the dichopore would be proportional to its cross-sectional area and, since the width is constant, capacity would be proportional to dichopore

depth. For constant velocities of in-current and out-current across a rhomb, slit length must be proportional to dichopore capacity. Dichopore depth is not readily measurable but in some instances e.g. *Staurocystis quadrifasciatus* (Pearce) (Pl. 137, fig. 1, text-fig. 32) slit length is almost exactly proportional to dichopore length. In the cryptorhombs of *Caryocrinites ornatus* Say (Pl. 138, fig. 3) the number of pores per sieve-pore cluster increases adaxially as does the total area of the entrance. The morphology of these rhombs would allow constant current velocities across the rhombs and within all dichopores, if currents were present. Ciliary currents are likely to have been of similar velocities in all dichopores.

It is more difficult to confirm the presence and direction of internal acceptor currents as they formed a closed current system, but there is some indirect evidence. In rhombs with closely spaced dichopores the inter-dichopore spaces were entirely within the boundary layer. Ciliary currents between dichopores would be expected on the same *a priori* grounds used to postulate their presence within dichopores. The width of dichopores was probably controlled by the combined thicknesses of ciliated epithelium, and lengths of cilia, lining them. If the dichopore width were much greater, dead water would accumulate within the dichopore. Alternatively cilia on opposite sides of the dichopore would interfere with each other if the dichopores were thinner. Where inter-dichopore widths equal dichopore widths both were probably controlled by the presence of cilia. This suggests that internal ciliated currents were present. The most efficient internal current is a counter-current.

Internal currents within a rhomb could only act efficiently if the external currents in all the dichopores were counter to them. With very rare exceptions in some incomplete cryptorhombs, current directions in all dichopores of one rhomb were apparently the same. Currents in all dichopores could have been counter to an internal current.

EXPLANATION OF PLATE 137

Stereophotos of disjunct pectinirhombs with confluent dichopores

Fig. 1. *Staurocystis quadrifasciatus* (Pearce). BU Ho1. L1:R5.

Figs. 2, 4. *Glansicystis baccata* (Forbes), typical form. GSM 7380. B2:IL2 (fig. 2) and L1:R5 (fig. 4).

Fig. 3. *Lipsanocystis traversensis* Ehlers and Leighley. UMMP 56222. L4:R3.

Fig. 5. *Schizocystis armata* (Forbes). GSM 7381. B2:IL2.

Figs. 6, 8. *Glansicystis baccata* (Forbes), common form. BU Ho55. L4:R3 (fig. 6) and L1:R5 (fig. 8).

Figs. 7, 9, 10. *Jaekelocystis hartleyi* Schuchert. BMNH E23121. L4:R3 (fig. 7), L1:R5 (fig. 9), and B2:IL2 (fig. 10). Note that the vestibules in IL2, L1, and L4 are small pores.

Figs. 1, 2, 4-10 $\times 3$, fig. 3 $\times 2$. All whitened with ammonium chloride sublimate.

EXPLANATION OF PLATE 138

Stereophotos of cryptorhombs

Fig. 1. *Hemicosmites* sp. RM Ec5364. Infra-lateral with simple pores.

Fig. 2. *Hemicosmites extraneus* Eichwald. RM Ec5283. Laterals with simple pores and radials with sieve-pores.

Figs. 3, 6. *Caryocrinites ornatus* Say. BMNH E29091. Internal (fig. 6) and external (fig. 3) views of isolated lateral plate. Note that the number of individual pores in a cluster increases towards centre of plate (fig. 3).

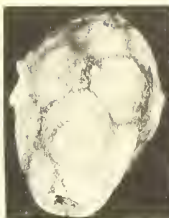
Fig. 5. *Hemicosmites* cf. *verrucosus* Eichwald. BMNH E15994. Infra-laterals and laterals. Note chimney-like simple pores.

Figs. 4, 7. *Caryocrinites ornatus* Say. BMNH E29084. Internal (fig. 7) and external (fig. 4) views of isolated infra-lateral plate. Note that only simple pores occur in the infra-lateral.

Figs. 1, 2 $\times 3$, figs. 3-7 $\times 2$. All whitened with ammonium chloride sublimate.



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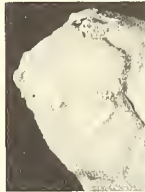
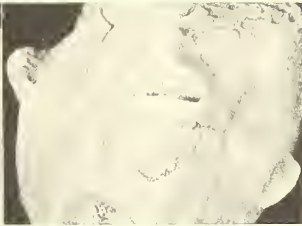
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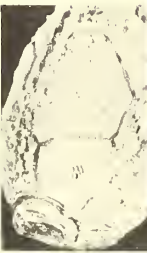
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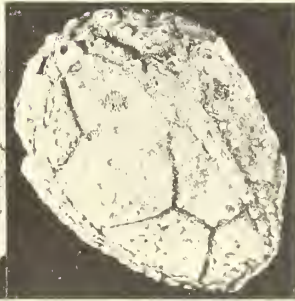
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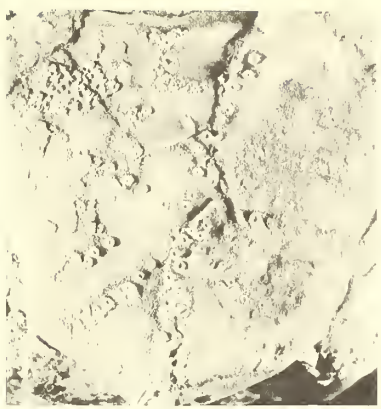


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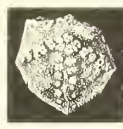




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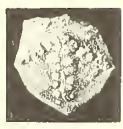
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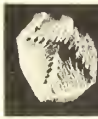
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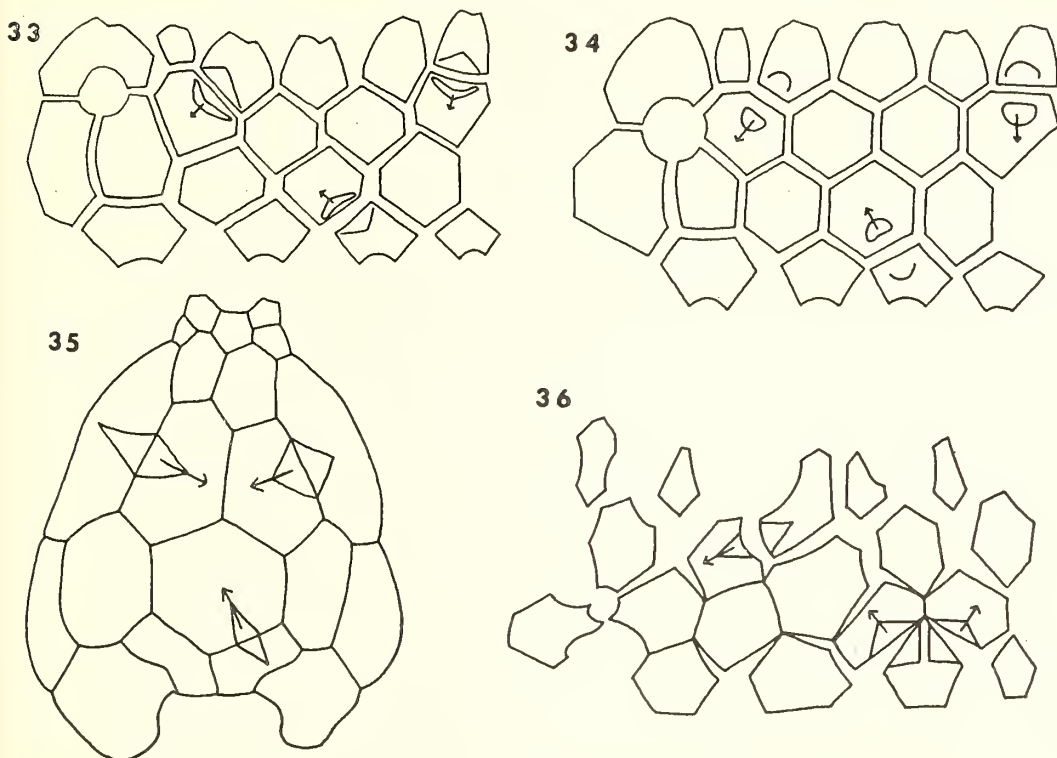
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In any cystoid relying on diffusion alone to distribute oxygenated fluids internally it would be advantageous to have rhombs over the entire external surface as all internal organs would be equidistant from an oxygen source. An approximation to this distribution of rhombs is found in *Cheirocrinus* and *Glyptocystites* (pectinirhombs) and in most cryptorhomb bearing genera. As the latter grew, relatively large areas without cryptorhombs were developed adjacent to the intra-circlet sutures of the infra-lateral and lateral



TEXT-FIGS. 33-6. Current directions in cystoids with three pectinirhombs.

33. *Staurocystis quadrifasciatus* (Pearce).

35. *Pleurocystites* sp.

34. *Glansicystis baccatus* (Forbes).

36. *Erinocystis* sp.

Note the current directions in all four have the same basic pattern. Plate outlines after Paul 1967a (text-figs. 33-4), Breimer 1963 (text-fig. 35), and Jaekel 1899 (text-fig. 36).

circlets. It is within just these areas that incomplete cryptorhombs develop relatively late in ontogeny. The distribution and development of cryptorhombs, and of pectinirhombs in *Cheirocrinus* and *Glyptocystites*, suggests that internal circulations were inefficient or lacking. Cystoids with only a few rhombs probably required some sort of internal circulation. Independent evidence for this is found in the Callocystitinae (Paul 1967b). In all cystoids with few rhombs the same external current pattern is found (text-figs. 33-6). This could reflect a fixed internal circulation but only if there were a constant relationship between donor and acceptor current directions. The most efficient relationship is a counter-current system.

As regards maintenance of a concentration gradient, there is considerable direct evidence for the presence of external currents within dichopores and some indirect evidence for internal counter-currents between dichopores. Again dichoporite pore-structures agree closely with the paradigm of an exchange system in this respect.

In general most details of dichoporite pore-structures agree remarkably well with the paradigm of an exchange system and would have been beneficial to exchange. Oxygen, and corresponding carbon dioxide, diffusion is the most likely form of this exchange and hence it seems that pectinirhombs and cryptorhombs were most probably respiratory organs.

D. EVOLUTIONARY AND TAXONOMIC IMPLICATIONS

The distribution of different types of pectinirhomb within the Glyptocystitida is summarized in text-fig. 37. Throughout the detailed functional analysis it was suggested that conjunct pectinirhombs were inherently less efficient than disjunct pectinirhombs (except in clearing the slits of extraneous particles) and that discrete dichopores were less efficient than confluent dichopores.

With the possible exception of *Scoliocystis* Jaekel, conjunct pectinirhombs are confined to the Cheiocrinidae and Pleurocystitidae. Their presence in the early (Arenig, L. Ordovician) cheiocrinids is probably primary. The appearance of conjunct pectinirhombs with confluent dichopores in later cheiocrinids like *Homocystites constrictus*

EXPLANATION OF PLATE 139

Stereophotos of cryptorhombs

Fig. 1. *Hemicosmites ualoni* Pander. RM Ec5517. Note the 'hidden rhombs'.

Fig. 2. *Hemicosmites* sp. RM Ec5702. Internal surface of isolated infra-lateral.

Figs. 3, 6. *Thomacystis tuberculata* Paul. BMNH E16300. Complete theca (fig. 3) and external mould of isolated basal plate (fig. 6). Latter shows cast of two dichopores which bifurcate near external surface of plate to form sieve-pore (cf. Pl. 140, fig. 5).

Fig. 4. *Caryocrinites roemeri* Jaekel. BMNH E29105. Infra-lateral and lateral plates; both show sieve-pores.

Fig. 5. *Caryocrinites septentrionalis* Regnéll. RM Ec25493. Note rims beside simple pores are more strongly developed than those by sieve-pores.

Fig. 7. *Caryocrinites ornatus* Say. SM A50958.

Fig. 8. *Hemicosmites* cf. *pyriformis* von Buch. BMNH E7592.

Figs. 1, 4, 8 $\times 2$, figs. 2, 3, 5-7 $\times 3$. All whitened with ammonium chloride sublimate.

EXPLANATION OF PLATE 140

Fig. 1. *Echinoencrinites angulosus* Pander. RM Ec5490, section 9. Vertical section through one dichopore in B2:IL2. Note structure of thecal plate. $\times 35$.

Fig. 2. *Pleurocystites filitextus* Billings. BMNH E7600b. Vertical section through B2:IL2 $\times 35$.

Fig. 3. *Cheirocrinus jamesii* (M'Coy). RSM 1870.12.879. External mould of isolated plate showing multi-disjunct pectinirhomb. $\times 6$.

Fig. 4. *Lipsanocystis magnus* Stumm. UI 32001. Detail of slits in L4:R3 to show microscopic bars across slits. $\times 25$.

Figs. 5, 6. *Hemicosmites* sp. nov. Sections through thecal plates to show sieve-pore (fig. 5) and simple pore (fig. 6). $\times 30$ approx.

Fig. 7. *Strobilocystites calvini* White. UI. Sutural view of isolated plate to show dichopores. Photographed under xylol. $\times 25$.

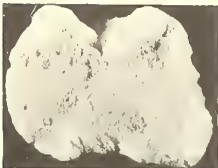
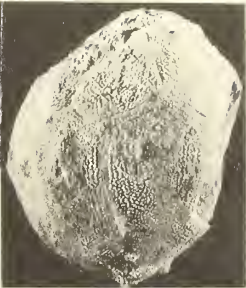
Fig. 8. *Echinoencrinites angulosus* Pander. RM Ec5490, section 3. Tangential section through B2:IL1 $\times 3$.



1



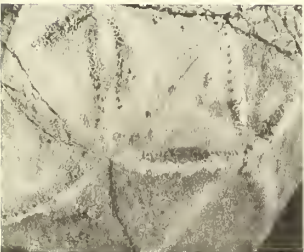
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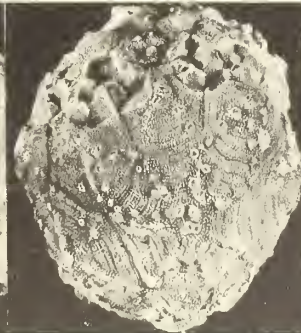
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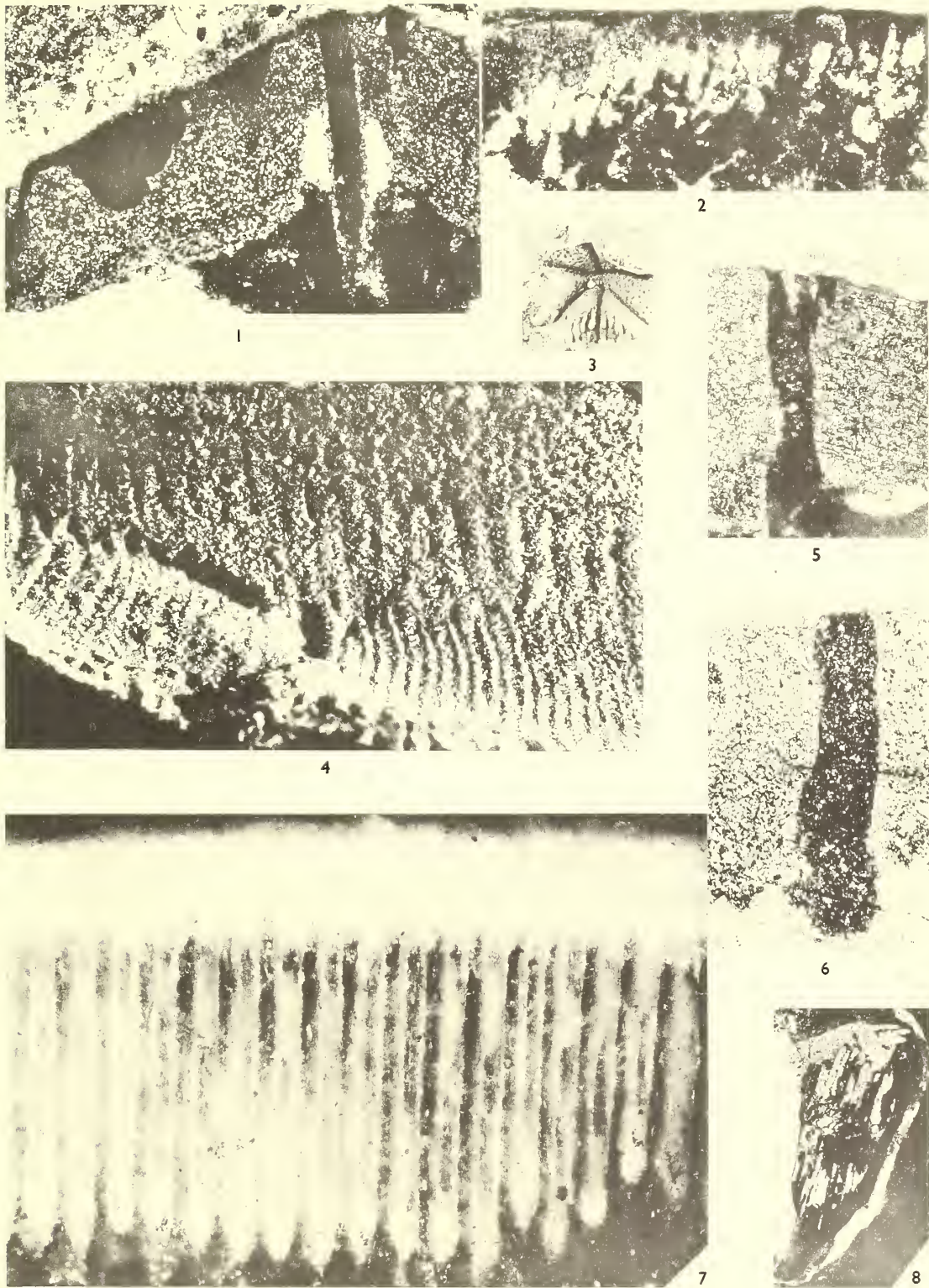


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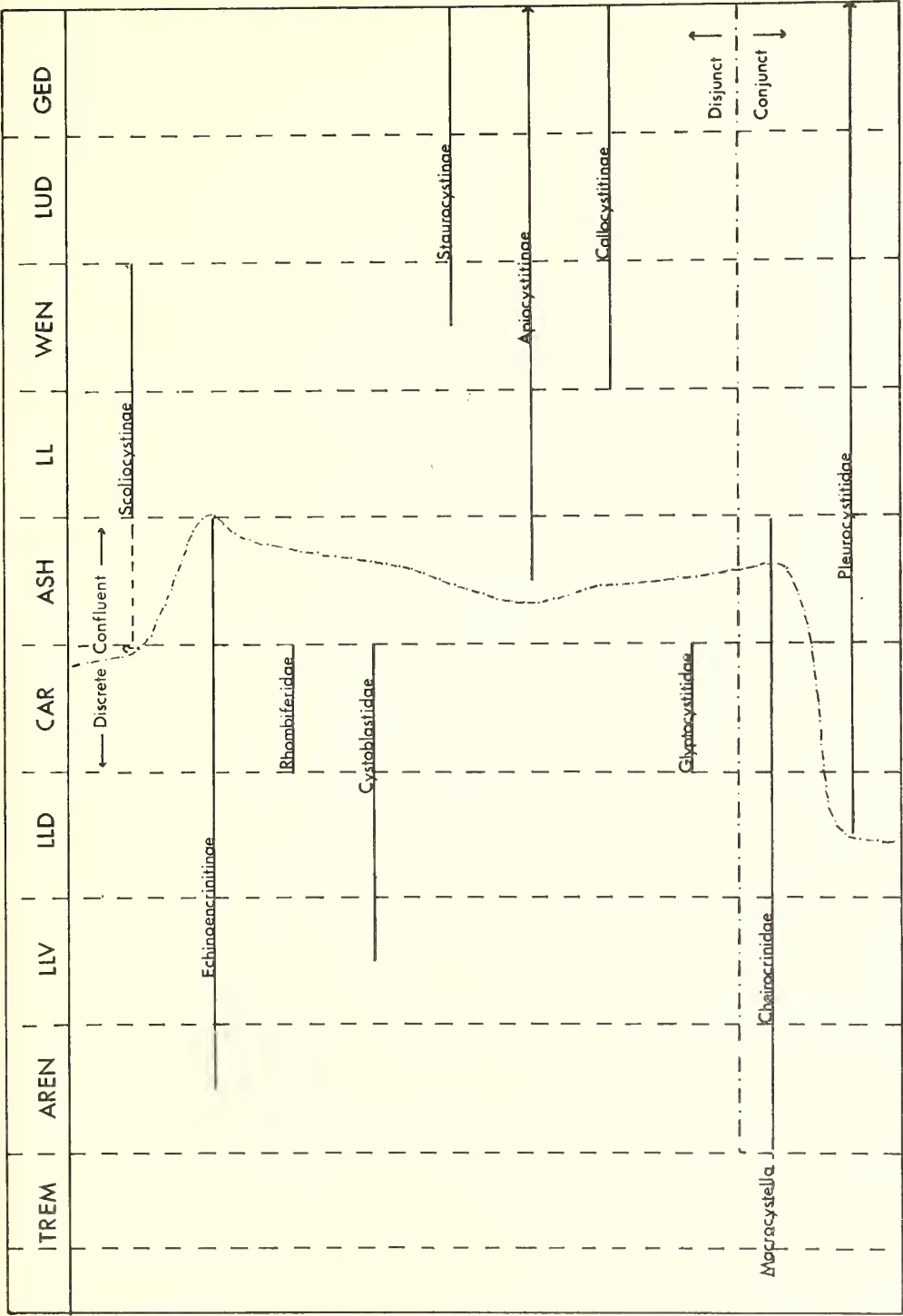


8





PAUL, Cystoid pore structures



TEXT-FIG. 37. Diagram to illustrate the stratigraphic range of the families of the Glyptocystitida, the distribution of conjunct and disjunct pectinirhombs and of confluent and discrete dichopores.

(Bather) (Ashgill, U. Ordovician), may be due to the mode of life. These pectinirhombs are more highly developed than those of earlier species. The retention of conjunct pectinirhombs in the Pleurocystitidae is probably due to the mode of life as suggested by Paul (1967c).

Confluent dichopores are unknown before the Llandeilo (M. Ordovician) while discrete dichopores are unknown after the Ashgill or possibly even the Caradoc (Late Middle Ordovician). Between these time limits there was a change from discrete to confluent dichopores independently in all evolutionary lines. The change may have been gradual in some cases: the pectinirhombs of *Glyptocystites* Billings are somewhat intermediate in character. All Silurian and Devonian glyptocystitids (with the exception of two species of Pleurocystitidae) have disjunct pectinirhombs with confluent dichopores, the most efficient type. Apparently throughout the evolution of the Glyptocystitida there was a progression from less to more efficient types of pectinirhomb. There is no evidence for a gradual change from conjunct to disjunct pectinirhombs but this is not surprising since it is difficult to see, on geometrical grounds, how a transition could exist.

At present no estimate of the functional efficiency of multi-disjunct pectinirhombs can be made. It is also much more difficult to compare the relative exchange efficiencies of pectinirhombs and cryptorhombs. The latter show much less variation and as yet no evolutionary trends have been recognized.

Within the Glyptocystitida (but not within the Rhombifera as a whole) there is evidence of a progressive decrease in the number of pectinirhombs in one theca. Bather (1913) explained this reduction in the Pleurocystitidae as a result of the anus partly taking over respiration. However, this explanation cannot be applied to the Callocystitidae, for example, which lack the extensive periproctal membrane supposedly used in respiration per anum. The reduction in the number of pectinirhombs could be due to the development of an internal circulation to distribute more efficiently oxygen gained from the pectinirhombs. Some independent evidence for such a circulation system has been described by Paul (1967b). The Glyptocystitida alone show this trend.

Rudwick (1961, 1964a) has emphasized that there may be a limited number of different structures which can perform a given function efficiently. In these cases it is inherently likely that the same or similar structures may have evolved independently several times. This was undoubtedly the case with confluent dichopores. It is also undoubtedly the case with rhombs as a whole. Fistulipores and dichopores represent basically different structures and there is no feasible way to evolve one from the other. The fistuliporite and dichoporite rhombs of the Rhombifera were independently acquired and the possession of rhombs is a polyphyletic character within the class. The Glyptocystitida and Hemicosmitida (dichoporite) can be separated from the Caryocystitida (fistuliporite) on several characters, e.g. plating arrangement, mode of growth, presence of true stem, besides the type of thecal canal present. The dichoporite superfamilies form natural units but it is still possible that they acquired their rhombs independently. It is easy to envisage that cryptorhombs evolved from disjunct pectinirhombs but there is no evidence at all for such a transition and both types of rhomb appear simultaneously in the Arenig. Furthermore, a rhomb-less ancestor for the Glyptocystitida is known (*Macrocystella*) which has an identical plate arrangement to later Glyptocystitida but which is quite distinct from all Hemicosmitida.

The cystoidea as currently understood (Kesling 1963, 1968) form a polyphyletic group

despite the recognition of the Eocrinoidea, Paracrinoidea, etc. as distinct classes. It is suggested that the Diploporita and Rhombifera should also be regarded as separate classes. Within the Rhombifera two orders, the Dichoporita (Jaekel 1899 emend.) and Fistuliporita nov., may be recognized. The former corresponds to the Pectinirhombifera (Delpy 1942, p. 207) but as the distinctive character is the possession of dichopores not pectinirhombs, an emended use of Jaekel's Dichoporita is preferred.

Since its first inception as a class to include all non-crinoid, non-blastoid Pelmatozoa, the Cystoidea has been subject to the removal of constituent groups as their distinctiveness was realized. This process is here carried to the limit and as neither Diploporita nor Rhombifera can be considered the more typical cystoids, the formal name Cystoidea must fall into disuse. The concept of a 'cystoid' is still useful in a general sense similar to that now reserved for 'Dinosaur'. Cystoid may be used to embrace the Eocrinoidea, Paracrinoidea, Rhombifera, Diploporita, Parablastoidea, Edrioblastoidea, and possibly the Blastoidea *s.s.* These classes share many common characteristics which separate them from 'carpoids' and 'edrioasteroids', two other groups once included within the Cystoidea *s.l.*

APPENDIX

List of species with dichoporite pore-structures examined.

Class Rhombifera Müller Order Dichoporita Jaekel emend. Superfamily Glyptocystitida Bather Family Macrocystellidae Bather emend. Jaekel	Rhomb type Pectinirhombs	
	slits	dichopores
<i>Macrocystella mariae</i> Callaway	—	—
<i>M. bohemicus</i> (Barrande)	—	—
<i>M. azaisei</i> (Thoral)	—	—
Family Cheiocrinidae Jaekel		
<i>Cheirocrinus</i> sp. (Ngwetung, Burma)	conjunct	discrete
<i>C. atavus</i> (Jaekel)	"	"
<i>C. giganteus</i> (Leuchtenberg)	"	"
<i>C. lauguedocianus</i> Thoral	"	"
<i>C. granulatus</i> (Jaekel)	conjunct and disjunct	"
<i>C. anatifornis</i> (Hall)	disjunct	"
<i>C. sp. nov.</i> (Tramore, Eire)	"	"
<i>C. sp.</i> (Katlino, U.S.S.R.)	"	"
<i>C. interruptus</i> (Jaekel)	multi-disjunct	unknown
<i>C. jamesi</i> (M'Coy)	"	"
<i>Homocystites alter</i> Barrande	conjunct	confluent
<i>H. constrictus</i> (Bather)	"	"
Family Echinoencrinidae Bather		
Subfamily Echinoencrinitinae Paul		
<i>Echinoencrinites angulosus</i> Pander	disjunct	discrete
<i>E. senckenbergii</i> von Meyer	"	"
<i>E. reticulatus</i> Jaekel	"	"
<i>Erinocystis</i> sp.	"	"
Subfamily Scoliocystinae Jaekel emend. Paul		
<i>Schizocystis armata</i> (Forbes)	"	confluent
<i>Glansicystis baccata</i> (Forbes)	"	"
<i>Osculocystis monobrachiolata</i> Paul	"	"

Family Rhombiferidae Kesling	slits	dichopores
<i>Rhombifera bohémica</i>	disjunct	discrete
Family Pleurocystitidae		
<i>Amecystis laevis</i> (Raymond)	—	—
<i>A. sp. nov.</i> (Neebish Channel, Michigan)	—	—
<i>Praepleurcystis watkinsi</i> (Strimple)	disjunct	confluent
<i>Pleurocystites elegans</i> Billings	conjunct	"
<i>P. filitextus</i> Billings	"	"
<i>P. squamosus</i> Billings	"	"
<i>P. rugeri</i> Salter	"	"
<i>P. quadratus</i> (Bather)	"	"
<i>P. gibbus</i> (Bather)	"	"
<i>Regulaecystis pleurocystoides</i> Dehm	"	"
Family Glyptocystitidae Bather		
<i>Glyptocystites ehlersi</i> Kesling	disjunct	?confluent
<i>G. multiporus</i> Billings	"	"
<i>G. regnelli</i> Sinclair	"	"
<i>G. batheri</i> Sinclair	"	"
Family Callocystitidae Bernard		
<i>Callocystites jewetti</i> Hall	"	"
<i>C. canadensis</i> Billings	"	"
<i>C. subglobosus</i> (Hall)	"	"
<i>Sphaerocystites multifasciatus</i> Hall	"	"
<i>S. bloomfieldensis</i> Schuchert	"	"
<i>Hallicystis imago</i> (Hall)	"	"
<i>H. elongata</i> Jaekel	"	"
<i>H. attenuata</i> Paul	"	"
<i>Lepadocystis moorei</i> (Meek)	"	"
<i>Brockocystis tecumsethi</i> (Billings)	disjunct	confluent
<i>Jaekelocystis hartleyi</i> Schuchert	"	"
<i>Lovenicystis angelini</i> (Haeckel)	"	"
<i>Apiocystites pentrematoides</i> Forbes	"	"
<i>Lepocrinites gebhardii</i> Conrad	"	"
<i>Prunocystites fletcheri</i> Forbes	"	"
<i>Lipsanocystis traversensis</i> Ehlers & Leighley	"	"
<i>L. magnus</i> Stumm	"	"
<i>Tetracystis fenestratus</i> Troost	"	"
<i>T. chrysalis</i> Schuchert	"	"
<i>T. oblongus</i> (Forbes)	"	"
<i>T. elegans</i> (Hall)	"	"
<i>Strobilocystites calvini</i> White	"	"
<i>Staurocystis quadrifasciatus</i> (Pearce)	"	"
<i>Pseudocrinites bifasciatus</i> Pearce	"	"
<i>P. pyriformis</i> Paul	"	"
<i>P. gordonii</i> Schuchert	"	"
<i>P. perdewi</i> Schuchert	"	"
<i>P. stellatus</i> Schuchert	"	"
<i>P. clarki</i> Schuchert	"	"
Superfamily Hemicosmitida Jaekel	cryptorhombs throughout	
Family Hemicosmitidae		
<i>Hemicosmites pyriformis</i> von Buch		
<i>H. extraneus</i> Eichwald		

H. sp. nov. (Kullsberg, Sweden)

cryptorhombs throughout

H. malum Pander

H. cf. verrucosus Eichwald

H. sp. (Karrast, Estonia)

H. sp. (Uxnörm, Estonia)

Family Caryocrinitidae Bernard

Caryocrinites ornatus Say

C. roemeri Jackel

C. septentrionalis Regnéll

C. elongatus (Rowley)

Family Thomacystidae Paul

Thomacystis tuberculata Paul

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C. R. C. PAUL
Geology Department
Indiana University Northwest
Gary, Indiana 46408
U.S.A.

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AUSTRALIRHYNCHIA, A NEW LOWER DEVONIAN RHYNCHONELLOID BRACHIOPOD FROM NEW SOUTH WALES

by N. M. SAVAGE

ABSTRACT. *Australirhynchia cudalensis* gen. et sp. nov., family Rhynchotrematidae, is described and figured from the early Siegenian Mandagery Park Formation, New South Wales.

STUDY of a Lower Devonian brachiopod fauna from the Mandagery Park Formation, near Manildra, New South Wales, has led to the recognition of a new rhynchonelloid genus, *Australirhynchia*. The Mandagery Park Formation consists of interbedded limestones and tuffaceous sandstones of probable early Siegenian age (Savage 1967, 1968). A silicified horizon within the basal limestone of the formation, 3 miles south of Manildra, at locality 1 of Savage (1968), contains a rich brachiopod fauna from which the material described herein has been selected.

SYSTEMATIC PALAEOLOGY

Superfamily RHYNCHONELLACEA Gray 1848
Family RHYNCHOTREMATIDAE Schuchert 1913
Subfamily ORTHORHYNCHULINAE Cooper 1956
Genus AUSTRALIRHYNCHIA nov.

Type species. Australirhynchia cudalensis sp. nov.

Diagnosis. A plicate rhynchonelloid with strongly angular costae which multiply by bifurcation on the dorsal fold and intercalation in the ventral sulcus. The dorsal interior has a small boss-like cardinal process between ponderous inner socket ridges. No median septum is present. The ventral interior is without distinct dental lamellae and the long heavy teeth, which are fused to the valve walls, bear deep longitudinal grooves.

Comparison. The ponderous inner socket ridges and small cardinal process, together with the massive, longitudinally grooved teeth and absence of distinct dental lamellae, suggest a relationship to the genera grouped as the Orthorhynchulinae by Schmidt (1965).

Of genera possessing a cardinal process but without a septalium the nearest is *Machaeraria* Cooper 1955, for this genus also lacks a dorsal median septum and has similarly long curved crura, crescentic in cross-section; moreover, there is a suggestion of bifurcation on the dorsal umbones of the specimens figured by Cooper, though this feature is much less prominent and more variable than in *Australirhynchia*. There are, however, several major differences; the outline of *Machaeraria* is more triangular with the greatest width anterior, and not posterior, of mid-length, the shell contours are more rounded, and the costae are more numerous. Internally the hinge plate of *Machaeraria* is deeply

cleft, the inner socket ridges are much smaller, and the teeth are less massive with no deep longitudinal grooves.

Another closely related genus is *Sicorhynchia* Havlíček 1961, from the Lower Devonian of Bohemia. This resembles *Australirhynchia* in lacking a septalium and a dorsal median septum. However, it differs greatly in general shell outline, being bluntly rounded posteriorly and very broad anteriorly with concave lateral margins. Furthermore, it does not possess the strongly inflated inner socket ridges and massive teeth of *Australirhynchia*.

Latonotoechia Havlíček 1961, also from the Lower Devonian of Bohemia, is another genus without a septalium and a dorsal median septum. In addition, it has massive teeth and inflated inner socket ridges (Havlíček 1961, p. 25, text-fig. 1). It is easily distinguished from the *Manildra* genus, however, for it has rounded contours quite unlike those of *Australirhynchia* and lacks the bifurcating and intercalating costae.

Of the genera referred by Schmidt (1965) to the Rhynchotrematinae, the Lower Silurian genus *Stegerhynchus* Foerste 1909, and the upper Silurian genus *Stegorhynchella* Rzhonsnitskaya 1959, both show a general resemblance to *Australirhynchia*. The *Manildra* form is distinct from these genera because of its unusual ornamentation and the absence of a median septum or callosity supporting the hinge plates. Moreover, both *Stegerhynchus* and *Stegorhynchella* have distinct umbonal cavities in their ventral valves, a feature completely absent from *Australirhynchia* where dental lamellae cannot be distinguished in any of the specimens examined.

Australirhynchia cudalensis sp. nov.

Plate 141

Material. Of a total of 167 silicified specimens 146 are complete shells with the valves conjoined. The remaining few specimens consist of 9 dorsal valves, 8 ventral valves, and 4 posterior fragments showing

EXPLANATION OF PLATE 141

Australirhynchia cudalensis gen. et sp. nov.

(All figures $\times 6$)

Figs. 1–4. Dorsal, ventral, posterior, and lateral views of SU 19579, a large specimen with a distinctly pentagonal outline, an emarginate anterior margin, and an anacline ventral interarea.

Figs. 5–9. Ventral, dorsal, lateral, anterior, and posterior views of SU 19578 (holotype).

Fig. 10. Ventro-anterior view of broken dorsal valve SU 19584 showing the small, rounded, posterior adductor scars and the larger, ovate, anterior adductor scars.

Figs. 11, 12. Dorso-anterior and dorsal views of specimen SU 19581, a ventral valve with the socket plates and cardinalia of the dorsal valve still attached to show the articulation. The small, rounded, adductor scar is prominent within the long, faintly impressed, diductor field.

Fig. 13. Dorsal view of broken ventral valve SU 19585 showing the deep delthyrial cavity bounded by long, thick, deeply grooved teeth from which the distal parts are broken.

Figs. 14–18. Dorsal, lateral, ventral, anterior, and posterior views of young specimen SU 19577. Here the maximum thickness is more posteriorly placed than in older specimens and the ventral interarea is distinctly apsacline.

Fig. 19. Ventral view of dorsal valve SU 19580 showing the small cardinal process between large inflated inner socket ridges, and the elongate adductor muscle field.

Fig. 20. Posterior view of specimen SU 19580 showing further the inflated inner socket ridges.

Figs. 21–5. Posterior, lateral, anterior, dorsal, and ventral views of specimen SU 19576, a young stage in which the bifurcation of the two central costae of the dorsal valve and the intercalation of two new costae in the ventral valve have just occurred. The fold and sulcus are poorly developed at this stage.

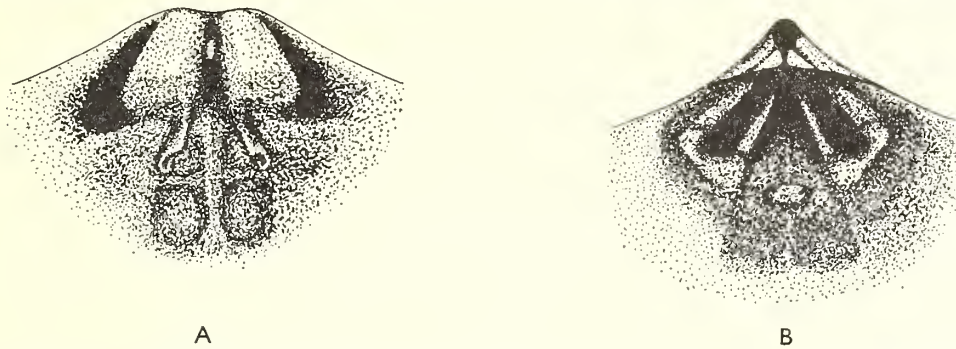


the valve articulation. The specimen numbers used are those of the Palaeontology Collection, Department of Geology and Geophysics, University of Sydney.

Holotype. Complete shell SU 19578.

Description. Exterior. In outline the shell is transversely ovate to subpentagonal with the greatest width at the hinge line. The cardinal margins are sharply rounded, the lateral margins are gently rounded, and the anterior margin is straight or emarginate. In lateral profile the shell is subequally biconvex with the greatest thickness between mid-length and the anterior margin (Pl. 141, figs. 4, 7).

The ventral valve is moderately convex with a strongly curved umbo and a prominent, suberect beak (Pl. 141, fig. 4). An apsacline to anacline interarea has a width about half the shell width and an apical angle of about 110° . The delthyrium includes an angle of



TEXT-FIG. 1. *Australirhynchia cudalensis* gen. et sp. nov. A. Interior of the dorsal valve showing the small cardinal process between the large inflated inner socket ridges. Note also the elongate adductor muscle field. B. Interior of the ventral valve showing the long, deeply grooved teeth and the small, rounded adductor field set within the larger diductor muscle field.

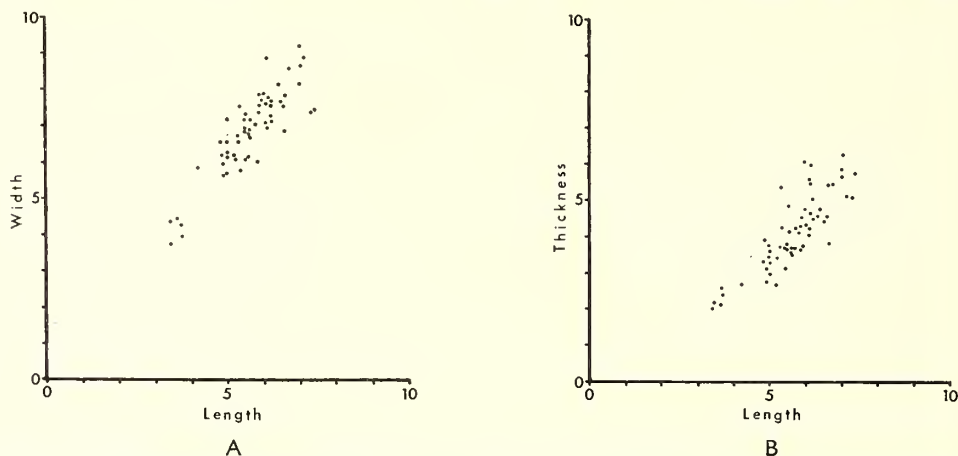
about 80° and is partly closed by small triangular deltidial plates. These roof over the dorsal umbo and almost meet to leave an oval foramen extending to the posterior extremity of the valve (Pl. 141, figs. 1, 6). The dorsal valve is strongly convex with a broad umbo and no interarea.

A broad ventral sulcus extends most of the valve length to the rectangularly uniplicate anterior commissure where it is bordered by very steep lateral walls (Pl. 141, figs. 5, 8). The dorsal fold is less pronounced posteriorly but very distinct anteriorly (Pl. 141, fig. 8). About 10–12 strong angular costae are present on the dorsal valve, with 4 on the fold, and about 9–11 costae are present on the ventral valve, with 3 in the sulcus. The costae on the fold invariably bifurcate to increase from 2 to 4 (Pl. 141, figs. 1, 6, 14, 24), whilst the single initial costa in the sulcus increases to 3 by an intercalation on either side (Pl. 141, figs. 2, 5, 16, 25). In both valves the increase occurs at about the 1.5 mm. growth stage. Numerous faint concentric growth lines cross the costae.

Interior of ventral valve. The ventral interior has a deep, narrow, delthyrial cavity bounded by long thick teeth, each bearing a prominent longitudinal groove with which the corresponding dorsal inner socket ridge articulates (Pl. 141, fig. 11). The teeth diverge anteriorly at about 45° . A long and anteriorly expanding diductor muscle field extends almost half the valve length (text-fig. 1B). The more strongly impressed adductor field

is very small and rounded, with a length about one-quarter that of the diductor field in which it is almost centrally placed (Pl. 141, fig. 12).

Interior of dorsal valve. The dorsal interior has a small boss-like cardinal process placed between large inflated inner socket ridges (Pl. 141, fig. 19). The sockets, which are small, triangular, and widely divergent, are bounded postero-laterally by the low overhanging valve margin. Thin, ventrally curved crura, which arise from the inside of the socket ridges, are slightly crescentic in cross-section with the convex side directed outwards (Pl. 141, fig. 19). No median septum is present. The adductor muscle scars are clearly



TEXT-FIG. 2. *Australirhynchia cudalensis* gen. et sp. nov. Scatter diagrams of the dimensions of 60 specimens plotted in mm. A. Plot of width to length. B. Plot of thickness to length.

impressed and extend about half the distance to the anterior margin (text-fig. 1A). Rounded, widely spaced, posterior adductors are separated from larger, longitudinally ovate anterior adductors by narrow, transverse ridges (Pl. 141, fig. 10).

Measurements (in mm.)

		<i>Length</i>	<i>Width</i>	<i>Thickness</i>
SU 19577	Complete shell	3.5	4.1	2.6
SU 19578	Complete shell	4.5	5.4	4.0
SU 19579	Complete shell	5.3	7.3	4.6
SU 19580	Dorsal valve	6.5	8.6	—
SU 19581	Ventral valve	6.0	7.6	—

Variation. Shells display little variation in external form apart from differences in thickness and width related principally to ontogeny (text-fig. 2). The multiplication of the costae by bifurcation on the fold and intercalation in the sulcus is invariably present and shows remarkably little variation. The costation on the flanks also shows a low variability so that in most shells the dorsal valve possesses 10 costae and the ventral valve 11 costae. Internally even the younger specimens show the massive teeth and socket ridges.

Ontogeny. A good range of growth stages has been collected and the later part of the ontogeny of the species can be followed in detail. In the youngest stage available the

maximum width occurs just anterior to mid-length, no bifurcation or intercalation of costae has occurred, and the ventral interarea is apsacline. At a slightly larger stage (Pl. 141, figs. 24, 25) the bifurcation of the two central costae of the dorsal valve and the intercalation of costae on either side of the central costa of the ventral valve is already apparent. As the shell approaches maturity it assumes a more pentagonal outline with the maximum width posterior to mid-length (Pl. 141, fig. 6). In a mature specimen the ventral interarea is distinctly concave and more anacline than apsacline. The maximum thickness of a mature specimen is well towards the anterior of the shell, largely because of the strong development of the dorsal fold and ventral sulcus (Pl. 141, figs. 7, 8). Internally, large inflated inner socket ridges and deeply grooved teeth are present in all but the youngest stages. In mature specimens the adductor muscle scars in both valves are deeply impressed.

Phylogeny. Although *Australirhynchia* is distinct from *Stegerhynchms* and *Machaeraria* in several important respects, these two genera appear to be the most closely related forms. It seems possible that both *Anstralirhynchia* and *Machaeraria* evolved independently from *Stegerhynchms*, although there is little evidence for this apart from the general morphological similarities mentioned above and the absence of possible alternative precursors during the Silurian. It is unlikely that *Australirhynchia* was derived from *Machaeraria* as it retains such features as inflated inner socket ridges and a relatively angular shell shape; features characteristic of *Stegerhynchms* but not present in *Machaeraria*.

Acknowledgements. The author would like to acknowledge the assistance of Professor C. E. Marshall and Dr. G. H. Packham of the Department of Geology and Geophysics, University of Sydney, where this work was commenced as part of a larger faunal study during the tenure of a Teaching Fellowship. It is also a pleasure to thank Professor F. H. T. Rhodes for his encouragement and for the use of facilities in the Department of Geology, University College of Swansea; also Dr. A. J. Boucot and Dr. J. G. Johnson of the California Institute of Technology for their helpful comments.

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N. M. SAVAGE
 Department of Geology
 University of Natal
 Durban S. Africa

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THE LLANDOVERY TRANSGRESSION OF THE WELSH BORDERLAND

by A. M. ZIEGLER, L. R. M. COCKS, and W. S. McKERROW

ABSTRACT. The study of the evolution of several brachiopod genera has enabled the early Silurian shelf sequences of the Welsh Borderland to be correlated with the type area of Llandovery, and, to some extent, with the graptolite zonal sequence. The transgression across the Borderland started at the beginning of Llandovery time, when areas in Montgomeryshire became inundated after a short break in deposition at the end of the Ashgill. The sea reached Shropshire, and possibly as far east as the Malverns and May Hill, by Middle Llandovery times. By late Upper Llandovery times, much of the English Midlands were covered.

Fossil communities indicate the relative depths in which the Llandovery sediments were deposited. With the advance of the sea, most sequences show a progressive increase of depth with time, although minor reversals are known. The many gaps in the local sequences are probably due to submarine erosion or non-deposition, rather than to uplift and sub-aerial erosion, because they are characteristically followed by progressively deeper-water communities. The community distribution indicates that a continuous gradient was maintained from the coast to the shelf margin, once the topographic relief of the original surface had been filled in.

DURING the Lower Silurian there was a spread of the shelf sea from Central Wales over the Welsh Borderland (text-fig. 1). Brachiopods are the dominant element in the shelf faunas of this region. Now that the evolution of several brachiopod genera is known in detail, it is possible to correlate the shelly deposits with the standard section at Llandovery.

Animal communities have been defined for this period, and they have been shown to reflect the depth of the sea. These communities are diachronous, and migrated as the transgression advanced.

The twin concepts, of evolving lineages as a basis for correlation and of animal communities as a basis for interpreting the environment, provide the foundation of this work.

BASIS OF CORRELATION

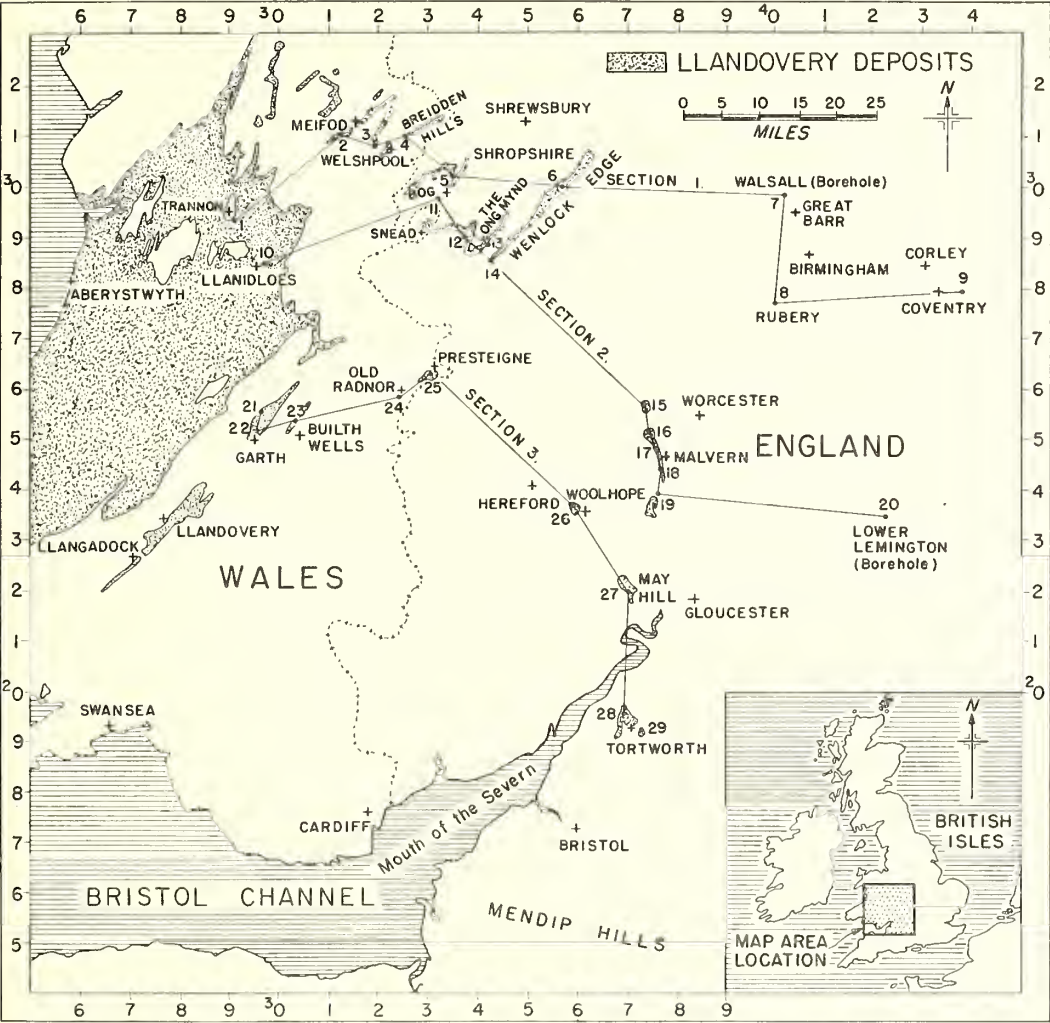
The type section of the Llandovery is to be seen south-east of the town of this name in Wales (Jones 1925). Brachiopods are the dominant faunal element in the area, but correlation of other shelly areas with the type section has had to await the study of the commoner brachiopod lineages. This approach contrasts with the tendency for workers in the shelf areas to have correlated Silurian beds by the assemblages of species present.

Evolutionary sequences are now known for the stricklandiids (Williams 1951, St. Joseph 1935), the pentamerids (St. Joseph 1938), the atrypide *Eocoelia* (Ziegler 1966b) and the strophomenide *Leptostrophia* (Cocks 1967a).

Some brachiopod lineages and their relationship with the type Llandovery are shown in text-fig. 2. The only brachiopods on this list which do not occur at Llandovery itself are *E. sulcata*, *C. lirata typica*, and *Pentameroides*; their assignment to C_6 is based on the fact that they are known to occur between C_5 and basal Wenlock beds in adjacent areas of the Welsh Borderland.

Most of the Lower Silurian of the British Isles carries a fauna of graptolites. Lapworth (1878) and Elles and Wood (1901-18) established a sequence of graptolite zones which

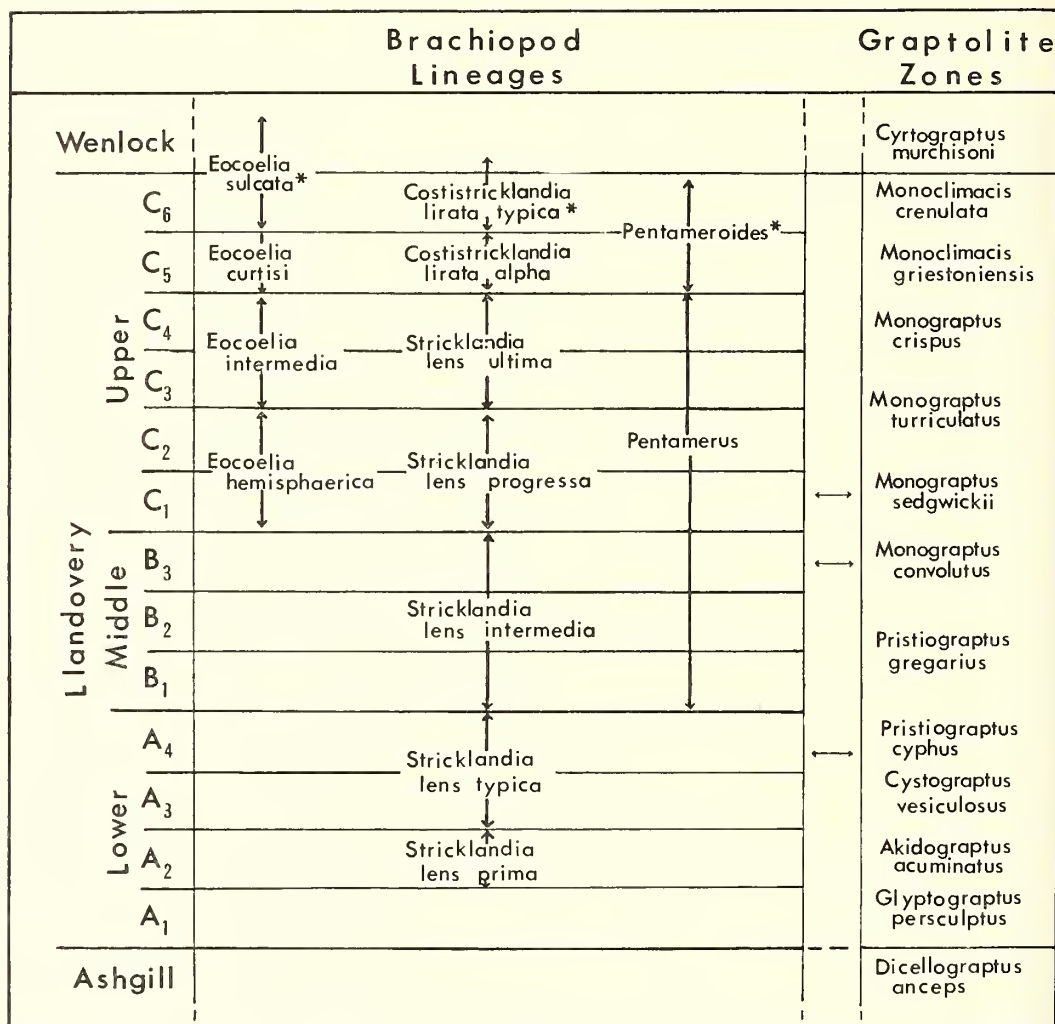
have provided an accepted basis for correlation. A few graptolites of zonal value have been found at Llandovery (text-fig. 2) but are only recorded from three horizons. Jones (1925, p. 360) found graptolites referable to his *acinaces* Zone in A₄ (this is now equated with the lower part of the *cyphus* Zone—Toghill 1968): Jones also (1949, p. 52) cor-



TEXT-FIG. 1. Location map of the Llandovery rocks of Wales and the Welsh Borderland, showing traverse lines and position of local sections.

relates B₃ with the *C. cometa* Band, which is in the upper part of the *convolutus* Zone; and he further records graptolites of the *sedgwickii* Zone (1925, p. 370) from beds assigned to C₁. This last fauna has been confirmed by our recent collecting from the other known locality of this restricted facies near an old ford across the River Sefin (Grid Ref. SN/7419 2811).

In addition to these finds from Llandoverly itself, other links between the brachiopod and graptolite sequences have been determined in the upper half of the Llandoverly of Shropshire (Cocks and Rickards, in press); but, as yet, firm ties are not proved for the whole Llandoverly succession.



TEXT-FIG. 2. The correlation of brachiopod lineages and graptolite zones with the standard sequence at Llandoverly. The asterisks against some brachiopods indicate that they have not been found at Llandoverly; the tie-arrows indicate graptolite finds at Llandoverly.

The limits of the Llandoverly Series at Llandoverly have not yet been properly defined, nor have they been firmly correlated with the sequence of graptolites. However, in this paper, we take the base of the series as equivalent to the base of the *Glyptograptus persculptus* Zone, and the top of the series at the base of the Wenlock; or as equivalent

to the base of the *C. nurchisoni* Zone, in the sense of Elles and Wood (1901–18). This last zone is sometimes now divided into a lower *Cyrtograptus centrifugus* Zone and an upper, restricted, *C. nurchisoni* Zone.

DISTRIBUTION OF ANIMAL COMMUNITIES

By means of large collections from single beds (many with over a thousand specimens), it is possible to quantify the proportions of species present at each locality.

Five main benthic animal communities have been defined by this means from the Llandovery (Ziegler 1965, Cocks 1967*b*, Ziegler, Cocks, and Bambach 1968). Each community is characterized by a particular faunal assemblage, consisting chiefly of brachiopods, and each has been named after a prominent brachiopod genus in the assemblage. They are the *Lingula* Community, the *Eocoelia* Community, the *Pentamerus* Community, the *Stricklandia* Community, and the *Clorinda* Community. At any one time, they occurred in this sequence, from the inferred coastline to the outer margin of the shelf. In beds of C₅ and C₆ age, *Pentamerus* and *Stricklandia* have evolved into *Pentameroides* and *Costistricklandia* respectively, and the community names change correspondingly.

So far the communities have been described only from the Upper Llandovery, but, apart from *Eocoelia*, the characteristic genera also occur in the Middle Llandovery, and the *Stricklandia* and *Clorinda* Communities are present in Lower Llandovery beds. A *Cryptothyrella* Community occurs in the Lower and Middle Llandovery with associates of the *Eocoelia* Community, and it appears to be an early equivalent of the latter community; it is abundant in basal beds at several areas, and occurs also in North America (Ziegler and Boucot, in press).

In addition, during parts of the Middle and Upper Llandovery, the position of the *Eocoelia* Community in Shropshire is taken by the parallel ? *Rostricellula* Community (Cocks and Rickards, in press). Also, in places near the edge of the shelf, the *Clorinda* Community dwindles to a sparser 'Marginal *Clorinda*' Community, with many typical members absent.

Apart from the burrowing *Lingula*, all the Llandovery brachiopods were epifaunal. Thus the majority of Silurian level bottom communities contrast with equivalent modern communities which are mainly infaunal. These Silurian communities were therefore less dependent on the type of substrate than their modern counterparts.

Rocky bottom communities are known at the base of some local sequences, although in all cases where these have been preserved they are accompanied by some soft-bottom elements.

The distribution of the main communities at three horizons in the Llandovery is shown in three maps at the end of the paper (text-figs. 12–14). While the actual depths represented by the communities are uncertain, the lines bounding them are presumed to parallel the bathymetric contours. Thus we have a picture of the changing configuration of the shelf sea during the transgression, and of the migration of the communities with time.

A distinction is drawn between 'basin' and 'graptolitic' facies. The former is restricted to areas (for example text-fig. 3, cols. 1 and 10) where rapid sediment supply, great

water depths, and considerable subsidence has resulted in large thicknesses of sediment. The term 'graptolitic' facies is used for rocks in which the dominant fossils are graptolites, and in which shelly forms, apart from a few orthocones and epiplanktonic bivalves, are generally absent. This facies represents one or other of two environments, firstly deposition under water which was too deep for benthic colonization at that time, or, secondly, water of any depth which had a foul bottom, lower temperature, or other physical conditions inimical to a shelly fauna. When a graptolitic facies occurs to seaward of a *Clorinda* Community, we feel justified in selecting the first of these alternatives, and interpreting the occurrence as being too deep for a shelly fauna; this situation applies to all of the Llandovery in the Welsh Borderland. However the second alternative certainly applied at other times and places during the Lower Palaeozoic, for example this is how we would interpret the Wenlock Shale to the south of the Long Mynd, Shropshire.

Acknowledgements. We are indebted to the late Professor W. F. Whittard for his advice, fossil collections, and loan of field maps. Dr. M. L. K. Curtis kindly made his thesis and collections available, and conducted us to localities in the Tortworth Inlier. Drs. W. B. N. Berry, R. B. Rickards, and P. Toghill identified the graptolites we have found, and discussed older records.

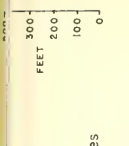
The theses by Ziegler (1963) and Cocks (1965), both at Oxford, were supported in part by the Burdett-Coutts Fund and the Department of Scientific and Industrial Research respectively. We are grateful to Mr. J. M. Edmonds and Mr. H. P. Powell for housing our thesis collections in the Oxford University Museum (Appendix 1), and for providing funds for their labelling. Collections made subsequently are deposited in the British Museum (Natural History) (Appendix 2) and the U.S. National Museum (Appendix 3). These last were prepared by Ziegler in the laboratories of Dr. A. J. Boucot at the California Institute of Technology from 1964-6. More recently, Ziegler has been supported by Grant 910-G from the Petroleum Research Fund, administered by the American Chemical Society; and by Grant GB-6592 from the National Science Foundation of America.

DESCRIPTIONS OF THE OUTCROPS

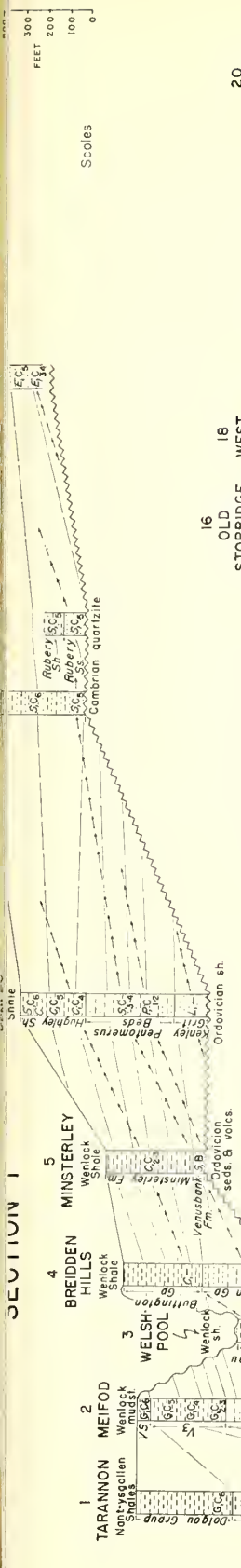
Three traverses across part of Wales and the Borderland (text-fig. 1) are represented by the composite sections in text-fig. 3.

In the following account, the areas studied in detail are treated first; i.e. the sections from Minsterley to Tortworth (text-fig. 3, cols. 5-6, 11-19, and 25-9). These constitute the classical Welsh Borderland area. Secondly, we discuss the small inliers to the east of the Borderland (text-fig. 3, cols. 7-9 and 20). We have examined collections from these areas, and include them for the sake of completeness. Finally we contrast these shelf sequences with areas to the west of the Borderland, which in Llandovery times formed the shelf margin and the basin. These areas are mostly in Wales (text-fig. 3, cols. 1-4, 10, and 21-3); we have collected in all of them, with the exception of the purely graptolitic sequences.

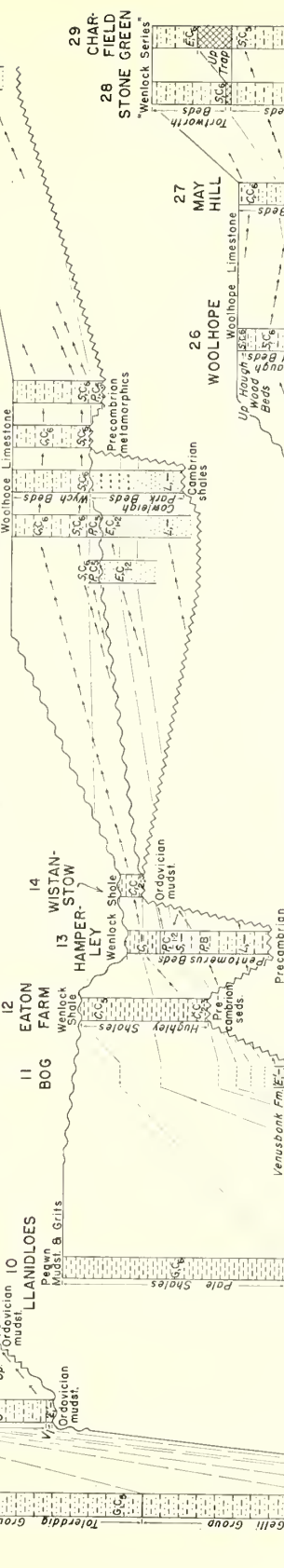
TEXT-FIG. 3. Three traverses across the Welsh Borderland (see text-fig. 1) showing local sections with communities, correlation, lithology, and stratigraphical relationships. True thicknesses are shown. The distances between columns are not the straight-line distances, but the N. 60° W. component of these distances.



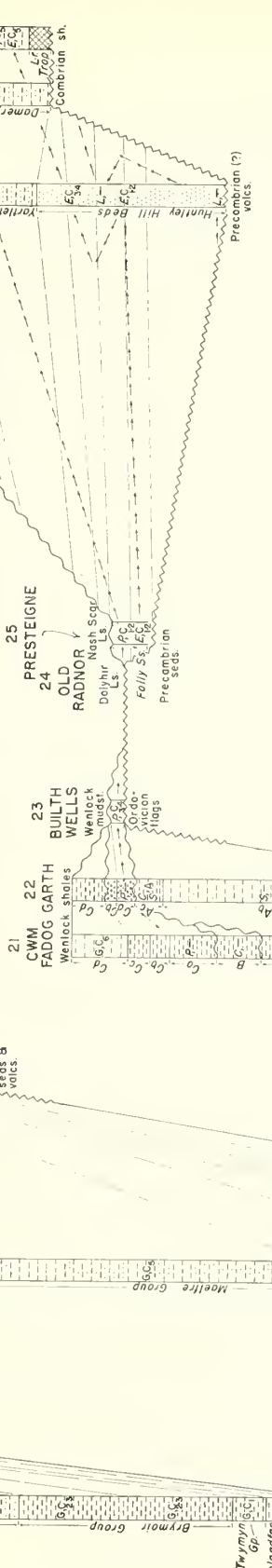
SECTION 1



SECTION 2



SECTION 3



Geological Facies

- G Graptolitic Facies
- C Clarinda Community
- S Stricklandia or Costisstricklandia
- P Pentamerus or Pentameroides
- E Eocella
- E' Cryptothyrella
- L Lingula

Stratigraphic Correlation

- C₁-C₆ Upper Llandovery
- B Middle "
- A Lower "
- Angular Unconformity
- Non-Sequence
- Conformable Contact
- "Time Line"
- "Community Path"

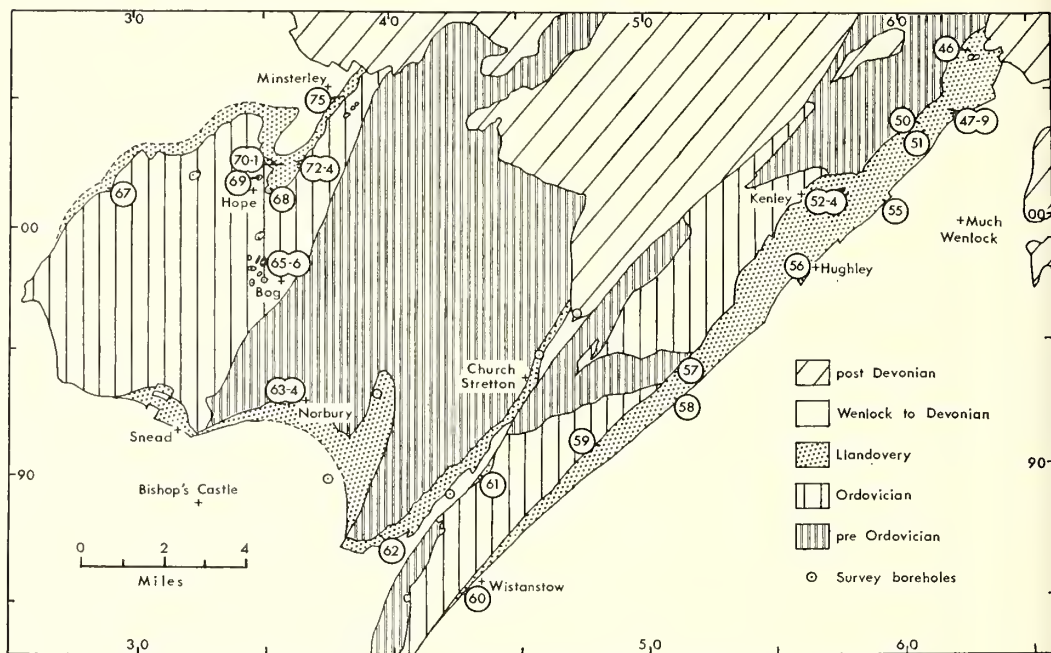
Lithology Legend

- Shale
- Shale & Sandstone
- Sandstone
- Conglomerate
- Volcanic Rock

MINSTERLEY AND BOG

Text-fig. 3, cols. 5 and 11

Exposures of Llandovery sediments to the north and west of the Shelfe Inlier, Shropshire (text-fig. 4), occur in a sinuous strip running north-east from north of Chirbury through Hope Valley and Venusbank to near Minsterley. Various outliers, including



TEXT-FIG. 4. Locality map of Shropshire (after many authors, with modifications).

those at Bog, rest unconformably on the Ordovician of the Shelfe Inlier. The area has been re-mapped, but the only major re-interpretation is based on new exposures indicating that the Venusbank 'outlier' is connected northwards with the outcrop in Hope Valley.

Whittard (1932) used the same stratigraphical names, i.e. Pentamerus Beds and Purple Shale, throughout Shropshire, but the Llandovery rocks of the Minsterley and Bog area differ in lithology and age from the beds in the Wenlock Edge outcrop (see below). Accordingly we propose new names: the Bog Quartzite, Venusbank Formation, and Minsterley Formation.

(a) *Venusbank Formation and Bog Quartzite.* The type section of the Venusbank Formation is in Hope Brook, running eastwards from near Hope Quarry. The base is exposed in both brook (SJ/3554 0207) and quarry (SJ/3550 0207), where a sandstone with occasional shale fragments rests on Hope Shales of Ordovician (Llanvirn) age. The top of the Formation in Hope Brook is taken above the highest of the dominant sandstones (SJ/3572 0215).

The base of the formation may also be seen in an outlier (SJ/3458 0146) two-thirds of a mile south-west of Hope Quarry (Tyler 1925). Here a basal conglomerate is present, in which pebbles (up to 5 cm.) of Hope Shales, Stapeley Volcanics (Llanvirm) and Stiperstones Quartzite (Arenig) occur. This outlier occurs at 900 ft. O.D. (Ordnance Datum—feet above sea level) but another small outlier is present 150 yards to the east, on the side of the valley and between 650 and 700 ft. O.D.; Hope Quarry lies at 600 ft. O.D., and, to the south-east, the Llandovery at Venusbank (SJ/3535 0125) is at 800 ft. O.D. Thus the conclusions reached by Whittard (1932, pp. 893–5), of an irregular base to the Llandovery of the area, are confirmed; steep dips are absent and there is no detectable subsequent faulting. It appears that the present-day Hope Valley has been re-excavated along the line of a pre-Middle Llandovery depression, and that the Llandovery sea spread over a surface relief of 200–300 ft. in this area. The thickness of the Venusbank Formation varies between 0 and 200 ft. (0–65 m.).

The formation is well exposed at Hope Quarry (SJ/3550 0207), where a thickness of 30 ft. (10 m.) is visible. Sandstone bands up to 3 ft. (1 m.) thick occur there, sometimes including shells or mudflakes at or near their base, with each unit fining up into unfossiliferous silts. Some of the sandstones have parallel laminae throughout, but cross-bedding is absent, apart from very occasional ripple cross-lamination on the tops of one or two sandstones. Unit bases are sharp, with no visible bottom structures apart from worm traces. Low-angle channelling occurs with occasional silty partings at the base of the channelling sandstone. These sediments may represent proximal turbidites filling a previously scoured channel of *Pentamerus*- and *Stricklandia*-Community depth.

The Llandovery also rests unconformably on the Ordovician in some poorly exposed outliers near Bog (SO/355 979) and at Round Hill (SO/348 993). Many large loose blocks of coarse quartzite are present; often containing pebbles and shale chips. These beds are termed the Bog Quartzite.

Fossil communities. The Hope Valley sections of the Venusbank Formation have mainly yielded fossils of the *Stricklandia* Community (Locs. 68–70, 72, 73); the exceptions are the presence of *Pentamerus* Communities at some places near the base of the formation (Loc. 74 and at SJ/3555 0107). This suggests that the irregular landscape was covered by a moderately deep shelf sea (*Pentamerus* Community) that soon became slightly deeper (*Stricklandia* Community). However, there may have been some fluctuation in depth, as Whittard (1932, p. 876) reports *Pentamerus* above *Stricklandia*-bearing beds in Hope Quarry.

In Ox Wood Dingle (Loc. 67), 4 miles west of Hope Valley, the *Stricklandia* Community is also present. However, early shallow-water conditions may be indicated at The Stubbs (2 miles north-west of Hope Quarry—SJ/324 033) where Whittard records (1932, p. 874) *Lingula* in growth position near the base of the Venusbank Formation.

The fauna of the Bog Quartzite (Locs. 65, 66) is a mixture of a near-shore *Cryptothyrella* Community with some rocky-bottom elements (Ziegler, Cocks, and Bambach 1968).

Correlation. All the collections from the Venusbank Formation and Bog Quartzite have yielded *Stricklandia*; the subspecies present at Bog is *S. lens intermedia* indicating a

Middle Llandovery age; the subspecies from the Venusbank Formation is at the boundary between *S. lens intermedia* and *progressa* and is B₃ to C₁ in age. A collection from near the base of Hope Quarry (Loc. 70) includes the graptolite *Climacograptus* aff. *rectangularis* (identified by R. B. Rickards), which indicates a Middle Llandovery age for the lower part of the formation. Whittard (1932, facing p. 896) records *Monograptus runcinatus pertinax* from the 'Pentamerus Beds of the Wilmington-Minsterley' area; this suggests that at least some of the Venusbank Formation is of early Upper Llandovery age.

(b) *Minsterley Formation*. The type section goes diagonally across the strike of the formation and is in Hope Brook. The base is taken above the top sandstone of the Venusbank Formation (SJ/3572 0215), and the top above the last purplish bed in the exposure to the south of Wagbeach (SJ/3642 0270). The thickness of the Minsterley Formation is about 400 ft.

The lowest beds seen are calcareous siltstones and mudstones, with occasional coarser beds; these represent a distinct sedimentary environment unknown elsewhere in the Welsh Borderland. They pass up into maroon, green, or blue mudstones, the top 150 ft. (49 m.) being of the same dominantly purple colour as the Hughley (Purple) Shales on the main Wenlock Edge outcrop. The mudstones contain some interbedded siltstone and bands of fragmented shells. Locally, the Minsterley Formation overlaps the Venusbank Formation, e.g. at Estell (Whittard 1932, p. 877) and east of Minsterley; in these areas the formation tends to be coarser. The Minsterley Formation is followed by several hundred feet of unfossiliferous turbidites, well exposed in Hope Valley, which may be either late Llandovery or early Wenlock in age.

Fossil communities. Collections in Hope Brook (Loc. 71) and Minsterley-Habberley Lane (Loc. 75) are both in the *Clorinda* Community; this indicates that the Minsterley Formation was deposited in deeper water than the underlying Venusbank Formation.

Correlation. The brachiopods collected from the Minsterley Formation provide no precise evidence of age, but Whittard's (1932, p. 877) record of graptolites from Locality 75 includes *Monograptus halli*, *M. becki*, and *M. cf. proteus*. This assemblage indicates a *turriculatus* Zone age (Cocks and Rickards, in press). A lack of fossils in the upper part of the formation, and in the overlying turbidites, makes it uncertain whether it terminates, even approximately, at the end of Llandovery time.

NORBURY AND CHURCH STRETTON

Text-fig. 3, cols. 12 and 13

A long winding outcrop of Llandovery rocks borders the south side of the Cambrian and Ordovician rocks of the Shelve Inlier, and continues all around the southern part of the Pre-Cambrian rocks of the Long Mynd (text-fig. 4). The formation names which we use for this area are the same as those used by Greig *et al.* (1968); the Pentamerus Beds and the Hughley (or Purple) Shales. The area, sometimes termed the southern Long Mynd-Shelve Outcrop, was mapped by Whittard (1932, pl. 59, 60) and more recently by the Geological Survey (Church Stretton Sheet, New Series, no. 166). Six

boreholes were drilled to assist the Survey in their mapping, and four of these passed through beds of Llandovery age (Cocks and Rickards, in press). These are called the Eaton Farm (text-fig. 3, col. 12) and Robury Ring Boreholes, both of which are to the west of the southern Long Mynd spur, and the Hamperley (text-fig. 3, col. 13) and Springbank Farm Boreholes, both of which are to the east of the Long Mynd spur and in the Church Stretton Valley. A fifth borehole, at Botvyle (also shown on text-fig. 4), did not penetrate to the local base of the Wenlock.

(a) *Pentamerus Beds*. Between Plowden (SO/382 874) and Little Stretton (SO/445 921), up to 60 ft. (20 m.) of conglomerates are intermittently present below mudstones and other sediments with *Pentamerus*. These beds, when fossiliferous, contain a *Lingula* Community, and, in parts, the formation name Kenley Grit (used in the adjacent Wenlock Edge outcrop—see below) might be employed. However, as the conglomerates fill quite small topographic pockets, and locally vary both in lithology and possible age, we follow Whittard (1932) and the Geological Survey (Greig *et al.* 1968) in treating these beds as a local coarse base to the *Pentamerus* Beds. The Hamperley and Springbank Farm Boreholes both revealed complete sections through the *Pentamerus* Beds, which are 480 (157 m.) and 170 ft. (56 m.) thick in the respective cores (although these thicknesses may be affected by minor faulting).

Whittard (1932) interpreted the basal deposits to the south of the Long Mynd as a beach with sea stacks. However, from faunal and sedimentological considerations, it seems more probable that most of the sedimentation occurred sub-tidally, and certainly a fairly deep-water *Pentamerus* Community was established at Hillend Farm (Loc. 62), only 20 ft. (7 m.) above the unconformity with the Pre-Cambrian.

The *Pentamerus* Beds are absent in the large embayment to the west of the southern Long Mynd spur (text-fig. 3, col. 12) and also south of The Roveries (SO/323 915); at both places Hughley Shale rests directly upon the unconformity. However, between these two places, at Norbury (Locs. 63 and 64), a local lens of calcareous sandstone, often crowded with *Pentamerus*, is present between the unconformity and the Hughley Shale, and this lens is termed 'Pentamerus Beds'. Further west, near Snead, Whittard (1932, p. 871) recorded 280 ft. of *Pentamerus* Beds, but his description shows that the lowest Silurian rocks contain a limited shelly fauna, perhaps representing an environment deeper than the *Clorinda* Community.

Fossil Communities. In the Hamperley Borehole, the *Lingula* Community is present between 65 and 115 ft. (21–38 m.) above the base (Cocks and Rickards, in press). This is followed by a ?*Rostricellula* Community, which is a parallel community to that of *Eocoelia*, and occupies a similar position, between *Lingula* and *Pentamerus* Communities. In the borehole, a *Pentamerus* Community succeeds the ?*Rostricellula* Community, and is itself succeeded by a *Stricklandia* Community. After the *Stricklandia* Community, there was a reversion to the *Pentamerus* Community immediately below the Hughley Shales. In the Springbank Farm Borehole, the *Pentamerus* Beds carry a *Pentamerus* Community throughout, although at approximately two-thirds up the formation, the proportion of *Stricklandia* increases enough to be termed a *Pentamerus*/*Stricklandia* mixture for that part of the core. This mixture was probably contemporary with the *Stricklandia* Community in the Hamperley Borehole.

In the surface exposures, the *Lingula* Community is developed in various parts of the basal coarse facies. At Marshbrook (Loc. 61) we have collected a mixed *Lingula*?*Rostricellula* Community. ?*Rostricellula* is a close homeomorph of *Eocoelia* and was listed as the latter by Whittard (1932, p. 864). *Pentamerus* Communities occur at Hillend Farm (Loc. 62) and at Norbury (Locs. 63 and 64). Further to the west, deeper water was present near Snead; above a basal *Pentamerus* Community, Whittard (1932, p. 872) records a fauna which we interpret as a 'Marginal' *Clorinda* Community.

Correlation. Graptolites from the Hamperley Borehole indicate the *convolutus* Zone for the middle part of the formation, with the *sedgwickii* Zone above. The *sedgwickii* Zone is also proved for the middle of the Springbank Farm core. The brachiopod collections from Hillend Farm and Norbury both contain *Eocoelia*, but the former locality carries *E. hemisphaerica* (indicating C_{1-2} age), while at Norbury *E. intermedia* is present (Ziegler 1966b), and indicates a C_{3-4} age for beds near the local base of the formation.

Whittard (1932, p. 872) records *Climacograptus* sp., *Monograptus halli* and *M. dextrorsus* from Snead; these indicate the *turriculatus* Zone. This evidence, together with Whittard's statement (1932, p. 873) that 'there is a gradation along strike from arenaceous to argillaceous sediments', points to a fairly rapid increase in depth westwards from the Long Mynd during C_{3-4} times. It also emphasizes that both base and top of the *Pentamerus* Beds are diachronous.

(b) *Hughley (or Purple) Shales.* These beds are not well exposed south of the Longmynd-Shelve Inlier. The Hamperley Borehole shows a thickness of 150 ft. (49 m.) and Whittard (1932, p. 866) estimated a thickness of 200–30 ft. of Hughley Shales to the south of the Long Mynd. To the west of the Long Mynd spur there is a greater thickness; 560 ft. (184 m.) is seen in the Eaton Farm borehole, although small faults may have affected this figure. Still further west, near Snead, Whittard (1932, p. 871) estimated that a minimum of 250 ft. were present. The formation is distinguished from the underlying *Pentamerus* Beds and overlying Wenlock Shale mainly by its colour, which is a characteristic maroon or purple, although green and brown bands also occur. The *Pentamerus* Beds are usually blue-hearted mudstones, and the Wenlock Shale grey and slightly siltier. The contacts between the formations are usually sharp.

Fossil Communities. Whittard (1932, p. 869) reports a *Clorinda* Community fauna between Plowden and Minton, and this community is also present in the Eaton Farm, Robury Ring, Hamperley, and Springbank Farm Boreholes. Above the *Clorinda* Community in the two boreholes to the west of the southern Long Mynd spur, a 'Marginal' *Clorinda* Community occurs, which probably indicates (Cocks and Rickards, in press) a continued deepening of the sea.

Correlation. Graptolites from the boreholes show a sequence from within the *turriculatus* Zone, through the *crispus* Zone and into the *griestoniensis* Zone. The top 75 ft. (25 m.) of the Hughley Shale in the Eaton Farm Borehole are above the *griestoniensis* Zone, but carry no diagnostic graptolites. Thus the presence or absence of the highest Llandovery *crenulata* Zone is not yet confirmed.

WENLOCK EDGE

Text-fig. 3, cols. 6 and 14

Llandovery rocks crop out in a strip twenty miles long, which parallels, and directly underlies, the rocks of Wenlock Edge (text-fig. 4). Whittard (1928) described this 'Main' outcrop in detail; the three formation names which he used, i.e. Arenaceous Beds, *Pentamerus* Beds, and Purple Shales, have been subsequently named by the Geological Survey Kenley Grit, *Pentamerus* Beds, and Hughley Shales. The northern part of this area was covered by the Shrewsbury Memoir (Pocock *et al.* 1938), and the southern part by the Church Stretton Memoir (Grieg *et al.* 1968). A recent revision of the northernmost part of the area was prompted by a very large temporary exposure at Devil's Dingle (Cocks and Walton 1968).

(a) *Kenley Grit*. A maximum thickness of 200 ft. (65 m.) is reached near Kenley itself (SJ/558 004). Four-and-a-half miles to the south-west, the Kenley Grit dies out near Gretton (SO/519 946). To the north-east, it thins more gradually, and is 35 ft. (11 m.) thick in Harper's Dingle (SJ/634 072), near the point where the Llandovery is covered by the Carboniferous, 6 miles from Kenley.

The formation consists of conglomerates, sandstones, arkoses, and some finer beds, but to the north-east there is no conglomerate except at the base; these basal pebbles are mainly derived from Uriconian rocks, but occasional Cambrian and Ordovician pebbles are present (Whittard 1928, p. 740). The formation rests with strong unconformity upon Ordovician and older rocks, and is distinguished from the overlying *Pentamerus* Beds by the abundance of coarse clastics and the absence of calcareous beds.

Fossil communities. The fossils recorded from the Grit (Whittard 1928, p. 741) all belong to the *Lingula* Community. *Lingula* itself occurs near the top of the formation at Morrellswood (near Loc. 46) and Sheinton Brook (near Loc. 50); it is also present in an old quarry near Kenley (Pocock *et al.* 1938, p. 106). An assemblage with abundant rhynchonellides, referable to the *Lingula* Community, but without *Lingula* itself, occurs at Cressage Park, two miles east of Kenley (Whittard 1928, p. 741).

Correlation. No fossils found in the Grit are of zonal significance; however, at Morrellswood (Loc. 46), beds of C₂₋₃ age occur immediately above the Grit, which must therefore be earlier.

(b) *Pentamerus Beds*. The Kenley Grit passes up gradationally into the *Pentamerus* Beds, but to the south-west, where the Grit is absent, the *Pentamerus* Beds rest unconformably upon Uriconian, Tremadoc, and Ordovician rocks. The *Pentamerus* Beds reach a maximum thickness of between 400 and 500 ft. (about 150 m.) in the north-eastern half of the area, and thin southwards to nothing in the vicinity of Wistanstow (SO/431 857). A *Pentamerus*-bearing conglomerate 1 in. thick has been reported (Whittard 1928, p. 749) in the bed of the Onny River (Loc. 60), but it is absent higher up on the river bank, where Hughley Shales rest directly upon the Ordovician. The lithology of the *Pentamerus* Beds consists of blue mudstones, with sporadic shelly limestones, and less fossiliferous siltstones and concretionary limestones. At the extreme northern end of the outcrop the 'Dingle Conglomerate' is seen near the base of the *Pentamerus* Beds in Harper's Dingle (SJ/6328 0704); the bed is confined to this one locality, and consists

of pebbles of Uriconian rock and *Pentamerus* shells set in a matrix of quartz sand and calcite (Whittard 1928, p. 745, Pocock *et al.* 1938, p. 107). Apart from this distinctive conglomerate, the *Pentamerus* Beds may be differentiated from the Kenley Grit by their palaeontology, finer grain size, and more calcareous sediments, but the contact between the two formations is gradational. The top of the *Pentamerus* Beds is usually sharp, with the colour change to the Hughley Shales, but the contact is sometimes confused by the presence of small turbidite bands (e.g. at Sheinton Brook—Loc. 51).

Fossil communities. A collection from near Gilberries (Loc. 57), in the lower part of the *Pentamerus* Beds, contains abundant *Hyattidina*. This genus does not fit precisely into any of the main Llandovery communities as at present defined (Ziegler *et al.* 1968), but abundant *Hyattidina* are associated with the *Eocoelia* Community in New York State and also at Presteigne (Locs. 90 and 93); we conclude that the Gilberries collection represents an intermediate environment between the *Lingula* Community of the Kenley Grit, and the deeper-water communities of the remainder of the *Pentamerus* Beds.

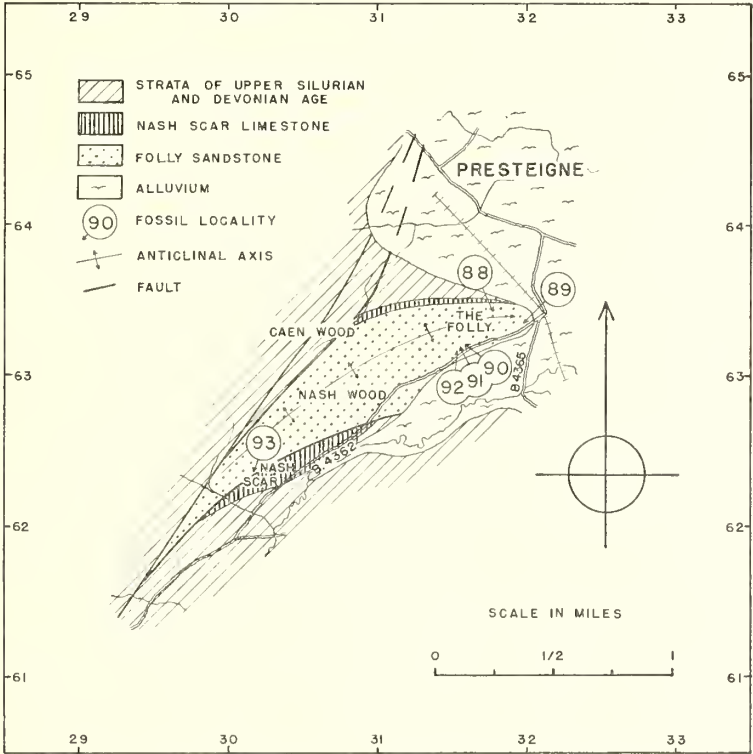
Collections from north-west of Merrishaw (Locs. 52 and 53) and near Ticklerton (Loc. 59) are typical of the *Pentamerus* Community. At about the centre of the outcrop, the deeper-water *Stricklandia* Community is present (Loc. 54) and in Sheinton Brook (Loc. 50), although this last collection only contains 1% of *Stricklandia*. At Morrellswood (Loc. 46) an assemblage dominated by *?Rostricellula* is present, this assemblage also occurs in the Church Stretton area (see above), where it is interpreted as a parallel community to that of *Eocoelia*.

Correlation. *Eocoelia heunisphaerica* indicates a C_{1-2} age for the *Pentamerus* Communities at Ticklerton (Loc. 59) and Merrishaw (Loc. 52). The *Stricklandia* Community at Sheinton (Loc. 50) and the collection from Merrishaw (Loc. 53) contain *S. lens ultima* of C_{3-4} age. Our evidence is thus consistent with a progressive increase of depth from C_1 to C_4 times during the deposition of the *Pentamerus* Beds of the Wenlock Edge Outcrop. Graptolites from various parts of the formation (Whittard 1928, Pocock *et al.* 1938) are all attributable to the *turriculatus* Zone, which is equivalent to C_{2-3} times.

(c) *Hughley (or Purple) Shales.* This formation has a thickness varying from 0 to 500 ft. (0–175 m.). The lithology is dominantly purplish mudstone, but occasional coarser turbidite bands also occur locally. The basal contact with the *Pentamerus* Beds is sharp and there is overlap on to the Ordovician to the south-east. North of Much Wenlock there is an apparently conformable upper contact with the Buildwas Beds; Cocks and Rickards (in press) conclude that these basal Wenlock beds may include equivalents of all the Lower Wenlock graptolite zones. However, as one proceeds south-west down the outcrop, the Middle Wenlock overlaps both the Lower Wenlock and the Hughley Shales and comes to rest unconformably on the Ordovician four miles south of the Long Mynd.

Fossil Communities. Most of the collections from the Hughley Shale of the Main Outcrop are typical of the *Clorinda* Community (Locs. 47–9, 51, 55, 56, 58, and 60), which reflects a deeper-water environment than that of the *Pentamerus* Beds. However, near the top of the formation to the north of the River Severn, Cocks and Walton (1968) describe a *Clorinda/Stricklandia* mixture, indicating some slight local shallowing in latest Llandovery times.

Correlation. The oldest brachiopod fauna collected from the Hughley Shale is from the very base of the formation in Sheinton Brook (Loc. 51), where *Eocoelia intermedia* indicates a C₃₋₄ age. *E. curtisi*, of C₅ age occurs in collections from Boathouse Coppice (Loc. 49) and Wall-under-Heywood (Loc. 58). *Costistricklandia lirata* and *Eocoelia sulcata* indicates a C₆ age for collections from Boathouse Coppice (Loc. 47), Domas (Loc. 55), and Hughley (Loc. 56), all very near the top of the formation. Thus the brachiopod evidence indicates that the formation spanned the period C₃ to C₆. Graptolites



TEXT-FIG. 5. Locality map of Presteigne, Radnorshire.

from the Onny River (Loc. 60) indicate the *turriculatus* Zone (probably equivalent to C₂₋₃); at several localities in the north-east part of the outcrop the *griestoniensis* Zone has now been proved. This last occurs in conjunction with C₅ indicators such as *Eocoelia curtisi*, and the probable presence of equivalents of the highest Llandovery *crenulata* Zone may be inferred by the presence of the C₆ brachiopods.

PRESTEIGNE

Text-fig. 3, cols. 24 and 25

To the south of Presteigne, Radnorshire, the Upper Llandovery crops out along the B4362 road between Nash Scar and the railway bridge near Corton (text-fig. 5); we propose the name Folly Sandstone for these beds. They are folded in an anticline with

its axis extending west-south-west through The Folly (SO/316 633). These Llandovery beds are overlain by a thin (15–20 ft.—about 6 m.) development of the Nash Scar Limestone to the north; to the south their contact is obscure, and the Folly Sandstone may either dip below or be faulted against the 200 ft. (65 m.) of limestone seen in Nash Scar Quarry. The outcrop is covered by drift east of The Folly, and is cut off by an extension of the Church Stretton Fault to the west of Nash Wood. The only published map of the area is the Geological Survey, Old Series, no. 56, NE. and SE., of more than a century ago; but it shows the Llandovery correctly, except for a possible fault north of Nash Scar quarry. The most recent description of these rocks was published in abstract form by Kirk (1951).

The Folly Sandstone consists of dark sandstones in beds ranging from a few inches to a few feet thick. There are many thin conglomerates with rounded pebbles up to $1\frac{1}{2}$ in. (4 cm.) in diameter. The thickness of the Folly Sandstone is in excess of 100 ft., but its base is not exposed. At Old Radnor, 4 miles to the south-west, this unit is missing altogether and Precambrian conglomerates and mudstones occur unconformably beneath the Dolyhir Limestone, the Old Radnor equivalent of the Nash Scar Limestone (Kirk, 1951, p. 56; Garwood and Goodyear, 1918, pl. vii). On the north side of the Presteigne inlier (SO/3152 6347), the contact with the Nash Scar limestone appears to be a disconformity; over an exposed distance of about 20 ft. the limestone rests on various sandstone beds indicating a relief of about 4 ft.

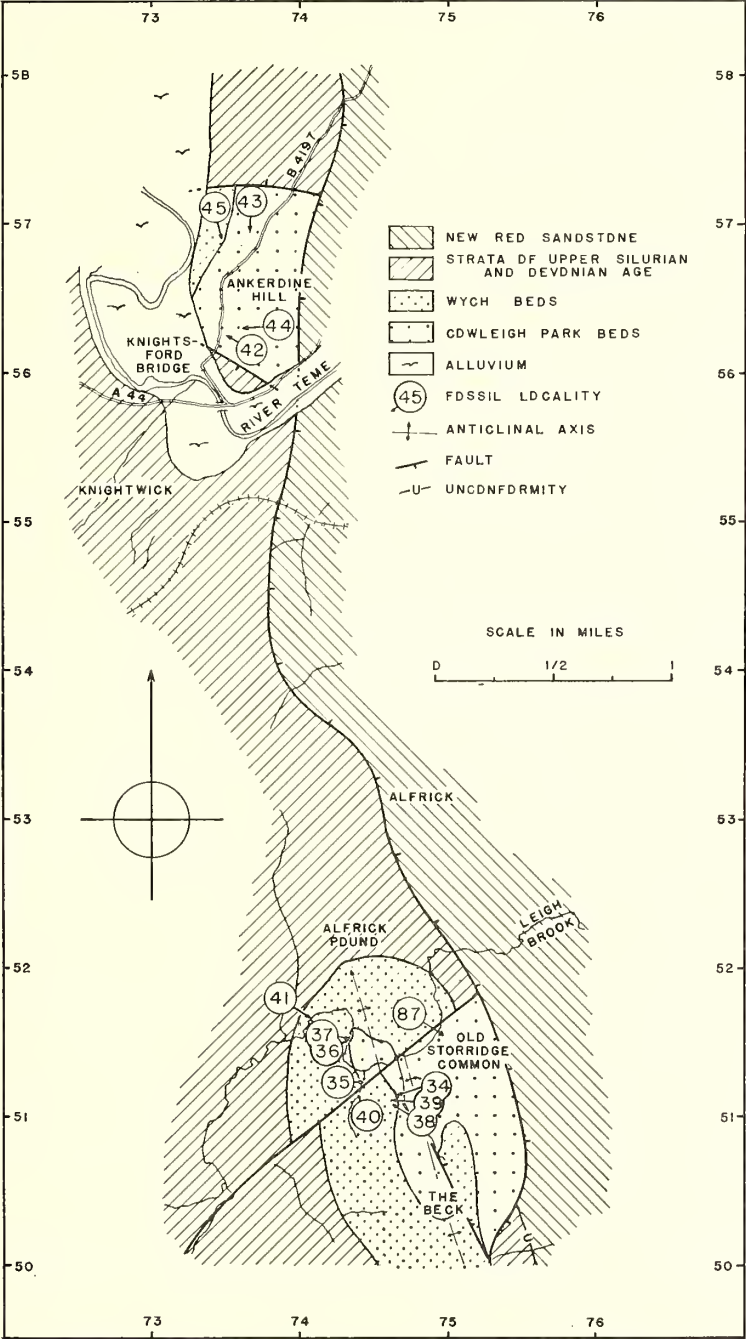
Fossil communities and correlation. The stricklandiids from this area have recently been described by Ziegler (1966a). Collections from above Nash Scar quarry (Loc. 93) and from south of The Folly (Loc. 90) yielded *Eocoelia hemisphaerica*; the latter locality also yielded *Stricklandia lens* aff. *progressa*. These collections are both representative of the *Eocoelia* Community and are both C_1 – C_2 in age. *Pentamerus* Community collections have been made in the Folly area (Locs. 91 and 92) from higher beds than Locality 90, but the presence of *E. hemisphaerica* shows they are also of C_1 – C_2 age. The *Pentamerus* Community is again present in Corton House Quarry (Loc. 89) and in Folly road a few feet under the base of the Nash Scar Limestone (Loc. 88); both these collections contain *S. lens* aff. *progressa* which shows that the top of the Folly Sandstone is still C_1 – C_2 in age.

The evidence from the Folly Sandstone shows that the Nash Scar Limestone could be as old as C_3 but the presence of *Rhipidium* (in the Garwood Collection, Geological Survey Museum) proves that part, at least, is Wenlock. An upper age limit is provided by the occurrence of *Cyrtograptus symmetricus* of Wenlock age in the overlying shales (Kirk 1951, p. 56).

ANKERDINE HILL AND OLD STORRIDGE COMMON

Text-fig. 3, cols. 15 and 16

Llandovery beds are exposed in a faulted block at Ankerdine Hill, $6\frac{1}{2}$ miles north of West Malvern, and again in the core of a north-plunging anticline at Old Storrige Common, 3 miles north of West Malvern (text-fig. 6). The base of the Llandovery succession is not exposed in either area. Groom (1910, p. 704) applied the terms, Cowleigh Park Beds, Wych Beds, and Woolhope Shales to the Llandovery rocks of the contiguous Malvern Hills area. However, the term Woolhope Shales is confusing and in any case this relatively thin unit cannot be distinguished with certainty from the Wych Beds.



TEXT-FIG. 6. Locality map of Ankerdine Hill and Old Storridge Common, Worcestershire.
This map is continuous with text-fig. 7.

We therefore reject the term Woolhope Shales for these Llandovery beds and regard the Wych Beds as extending up to the first appearance of the dominantly calcareous beds of the Woolhope Limestone. The latter is a gradational contact and could, of course, be diachronous.

(a) *Cowleigh Park Beds*. Fine green sandstones and siltstones make up the lowest beds exposed on Ankerdine Hill, while at Old Storridge Common the sediments are coarser and thicker bedded (up to 2 ft.) sandstones. Lack of exposures and the presence of faults make thickness estimates very uncertain; minimum exposed thicknesses are about 200 ft. (65 m.) at Ankerdine Hill and 400 ft. (130 m.) at Old Storridge Common.

Fossil communities. In the Old Storridge Common area, fossils diagnostic of the *Lingula* Community have been recorded by Lamont and Gilbert (1945, p. 642) near the axis of the anticline, and therefore probably low in the Cowleigh Park Beds. The *Eocoelia* Community occurs within a few feet of the top of the formation in Leigh Brook (Loc. 36) and in a north-flowing tributary (Loc. 35). It also occurs in lower beds south of Leigh Brook (Locs. 34 and 87). At Ankerdine Hill, the *Eocoelia* Community is represented in all three collections obtained (Locs. 42–4), but the relative stratigraphic positions of these are not known.

Correlation. All the *Eocoelia* obtained from the Cowleigh Park Beds at Ankerdine Hill and Old Storridge Common are *E. hemisphaerica* of C_1 – C_2 age; the type of this species comes from Ankerdine Hill (Ziegler 1966b). The lower beds with the *Lingula* Community may either be of a very early Upper Llandovery or a late Middle Llandovery age.

(b) *Wych Beds*. The Wych Beds consist of shales with some siltstones (less than 10% of the formation). The base is exposed in Leigh Brook (Loc. 37) near the disused Gunwich Mill (SO/7430 5152) west of Old Storridge Common. The contact is sharp, but, although there is palaeontological evidence of a non-sequence, there is no sign of erosion of the underlying Cowleigh Park Beds. The formation appears to be about 400 ft. (130 m.) thick in the section west of Gunwich Mill.

Fossil communities. The basal few feet of Wych Beds at Gunwich Mill (Loc. 37) contain a *Pentameroides* Community. The non-sequence at this locality is thus followed by deeper-water conditions than in the *Eocoelia* Community of the Cowleigh Park Beds. The evidence suggests a progressive increase in water depth throughout Upper Llandovery times with a long pause in sedimentation at this locality before the deposition of the finer grained Wych Beds. A *Pentameroides* Community has also been obtained from loose blocks on Ankerdine Hill (Loc. 45) and may represent a similar low horizon in the Wych Beds.

The *Pentameroides* Community is followed by the *Costistricklandia* Community some 10 or 20 ft. (about 5 m.) above the base of the Wych Beds; collections low in the formation were obtained from a track in Coneygore Coppice (Locs. 38, 39) and in a north-flowing tributary of Leigh Brook (Loc. 40) to the south and south-west of Old Storridge Common. A continued increase in the depth of water is indicated by the occurrence of the *Clorinda* Community near the top of the Wych Beds to the north-east of Mousehole Bridge (Loc. 41).

Correlation. The basal Wych Beds at Gunwich Mill contain *Eocoelia curtisi*, showing that these beds are of C₅ age and that the non-sequence covers the whole of C₃ and C₄ time. The collection from Ankerdine Hill also contains *E. curtisi*.

The highest Wych Beds near Mousehole Bridge yield *E. sulcata* of C₆ age. No fossils of C₆ age have been collected on Ankerdine Hill, and it is probable that the higher parts of the Wych Beds have been cut out by faulting.

MALVERN HILLS

Text-fig. 3, cols. 17, 18, and 19

Llandovery rocks crop out continuously from Old Storridge Common south through West Malvern to Herefordshire Beacon (text-fig. 7). They appear again south of Herefordshire Beacon in the area to the east of Eastnor (text-fig. 8). As in the Old Storridge Common area, we recognize two formations, the Wych Beds (named from The Wyche 1½ miles south of West Malvern) and the Cowleigh Park Beds (Cowleigh Park, 1 mile north of West Malvern contains many small exposures of this lower formation). This area has been mapped by Groom (1899, 1900) and by Phipps and Reeve (1967). We differ from these authors in our interpretation of the Llandovery in two main respects: the upper limit of the Wych Beds is taken immediately below the Woolhope Limestone (see above); and we have no doubt that an unconformity is present below the Silurian along the west side of the Malverns (Reading and Poole 1961, 1962, Ziegler 1964). The Cowleigh Park Beds rest on Cambrian shales east of Eastnor and probably again east of Cowleigh Park; to the south-east of Cowleigh Park they are inferred to rest on Malvernian. Between West Malvern and Ragged Stone Hill (at the south end of the Malvern Hills—SO/759365) the Cowleigh Park Beds are overlapped by the Wych Beds which rest directly on the Malvernian.

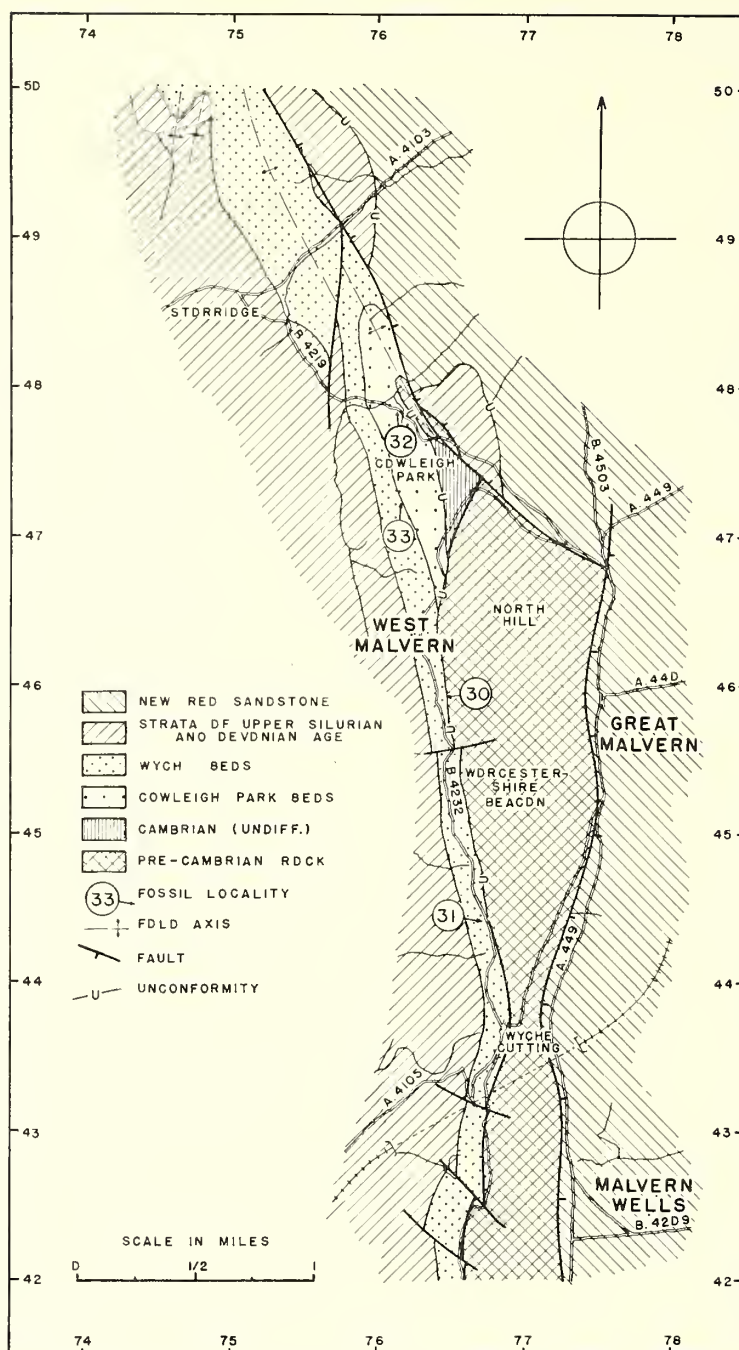
(a) *Cowleigh Park Beds.* Exposures of this formation are scattered, but our mapping suggests that there are at least four distinct members:

1. A basal member of up to 15 ft. (5 m.) of red micaceous mudstone interbedded with several thin (4 in. (10 cm.) or less) green sandstones composed of round quartz grains about 1 mm. in diameter. These were exposed during a Geologist's Association field trip in 1963, leader Mr. N. E. Butcher, with the aid of a mechanical digger, near the base of the Silurian to the south-west of Bronsil Castle.

2. About 100 ft. of light brown siltstones and sandstones containing fossils of the *Lingula* Community and occasional pebbles of Malvernian rock. This lithology crops out in both Cowleigh Park and in the Eastnor Obelisk—Howler's Heath area (Loc. 32, 23, and 24).

3. A coarse pink sandstone about 100 ft. (33 m.) thick which forms a ridge extending south-south-east from Rough Hill (SO/758 482) into Cowleigh Park. A similar topographic feature extends from Eastnor Obelisk to the eastern margin of Howler's Heath, and, though there are no outcrops there, loose blocks of a similar pink sandstone occur, containing chips of Cambrian shale.

4. Up to 200 ft. (65 m.) of unsorted purple conglomerates with angular pebbles up to 3 cm. in diameter, interbedded with coarse green sandstones up to a foot thick. This unusual lithology is known only from Cowleigh Park (SO/7616 4723) and may be restricted to this area which is immediately adjacent to the Malvernian ridge source area.



TEXT-FIG. 7. Locality map of the northern Malvern Hills, West Malvern, and Cowleigh Park areas. This map is continuous with text-figs. 6 and 8.

To the south-west of the Malverns, Holl (1865, fig. 4) and Groom (1899, p. 167) have described the unconformable relationship at the base of the Cowleigh Park Beds where the Llandovery rocks rest on the Tremadocian Bronsil Shales between the Obelisk and Howler's Heath. Although Cambrian shales have never been mapped to the north-west of the Malverns, it is probable that a similar unconformity exists in the Cowleigh Park area; Groom (1900, p. 157) states that Cambrian shale was exposed in a well 1 mile north of West Malvern, near the foot of North Hill. Our interpretation of the geology is given in text-fig. 7.

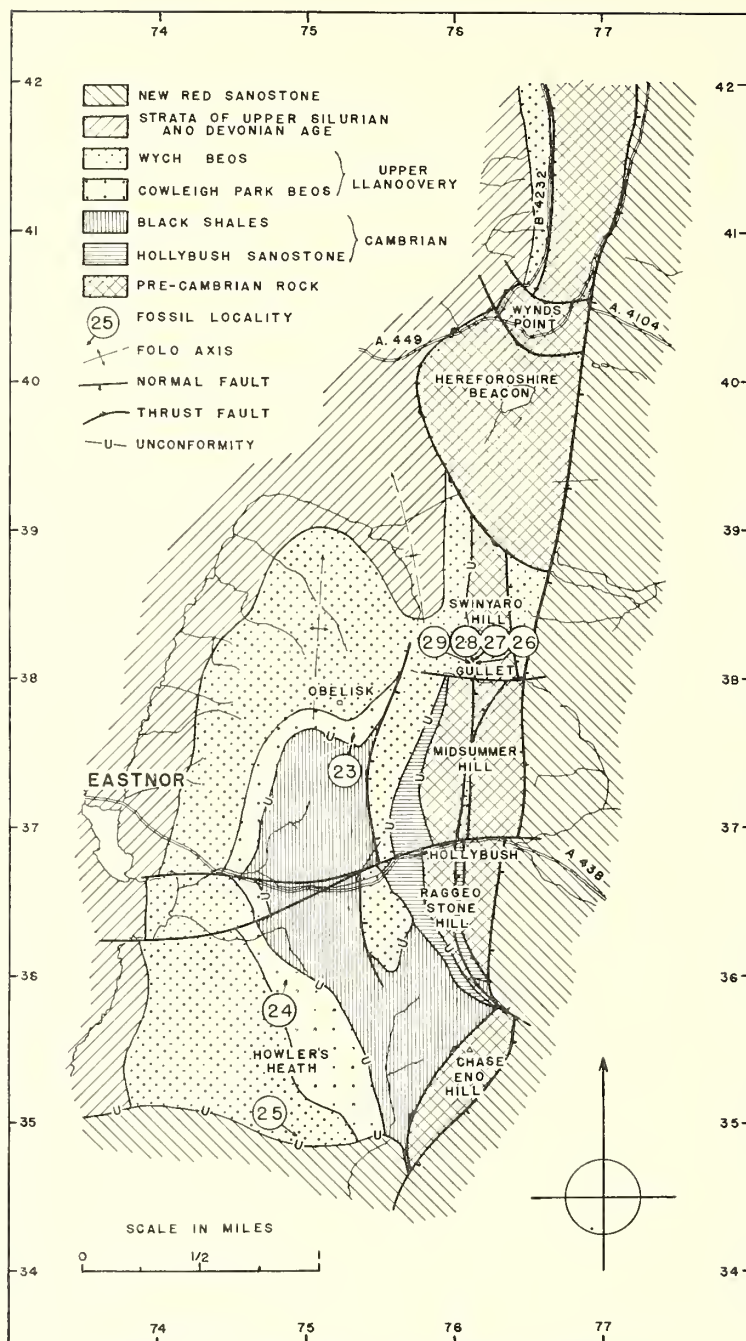
The pebbles in the conglomerates show that a landmass composed of Malvernian and Cambrian rocks was being eroded—this source area may have extended eastwards from the present-day Malvern Hills. The thickness of the Cowleigh Park Beds is perhaps 250 ft. (80 m.) at the Eastnor Obelisk. At Cowleigh Park there is probably between 350 and 400 ft. (100–30 m.), but lack of exposures and the possible presence of faults make this estimate uncertain.

Fossil communities. The *Lingula* Community is the only fossil community represented in the Cowleigh Park Beds of the Malverns; the fossils are confined to the second (siltstone and sandstone) member. They have been collected from Cowleigh Park (Loc. 32), south of the Obelisk (Loc. 23), and north of Howler's Heath (Loc. 24). This community indicates very shallow marine conditions, and it is possible that some of the Cowleigh Park Beds are beach deposits. The coarseness of the sediments and the absence of the *Eocoelia* Community indicate environments nearer to the shore-line than those in correlated beds to the north-north-west near Old Storridge Common and Ankerdine Hill, and to the south-south-west at May Hill.

Correlation. No fossils of value in correlation occur in the Cowleigh Park Beds of the Malverns. Comparison with Old Storridge Common to the north and with May Hill to the south suggests an early Upper Llandovery or late Middle Llandovery age.

(b) *Wych Beds.* The Wych Beds are seen resting on the fourth (conglomerate) member of the Cowleigh Park Beds at the Cowleigh Park football field (SO/7616 4723); the basal 6 ft. (2 m.) are coarse sandstones (they appear to be re-worked Cowleigh Park Beds) with occasional broken *Pentameroides*, which probably indicate a deeper-water environment than in the Cowleigh Park Beds; these sandstones are followed by shales and green siltstones typical of the main mass of the Wych Beds. The only other two exposures of the base of the Wych Beds are on the western margin of the Malvern Hills at West Malvern (SO/7646 4554) commonly known as the Sycamore tree quarry (Robertson 1926, p. 168), and the Gullet Quarry (SO/7612 3811) (Reading and Poole 1961); at both these places a basal conglomerate is present, up to 2 or 3 ft. (1 m.) thick. The conglomerate consists of rounded boulders of various Malvernian rocks, ranging from 4 mm. to 80 cm. in diameter, set in a matrix of green siltstone and mudstone—typical of the Wych Beds—containing a rich fauna of brachiopods and corals (see below).

The Wych Beds are poorly exposed and their thickness is determined with difficulty; estimates of about 400 ft. (130 m.) have been obtained from sections near Eastnor Obelisk and in Cowleigh Park. This is about the same thickness as at Old Storridge Common. It includes all the beds up to the base of the Woolhope Limestone, that is, where calcareous nodular beds become abundant.



TEXT-FIG. 8. Locality map of the southern Malvern Hills.
This map is continuous with text-fig. 7.

Fossil communities. The fossils in the matrix of the conglomerates at West Malvern (Loc. 30) and the Gullet Quarry (Loc. 26) contain many species that are absent elsewhere in the Upper Llandovery of the Welsh Borderland, apart from Bog, Shropshire, and are interpreted (Ziegler, Cocks, and Bambach 1968), as a mixture of rocky bottom and soft bottom animals. Rocky bottom communities are usually in the areas of erosion, and do not frequently get preserved, but in this case the beds immediately above the conglomerate at the Gullet Quarry contain a *Pentameroides* Community (Loc. 27), and the fauna on the rounded boulders probably lived well below low-tide level and uncovered by sediment for a long period.

At Cowleigh Park (SO/7616 4723) the basal 6 ft. (2 m.) of the Wych Beds are coarse sandstones containing broken *Pentameroides*, and at the same exposure (Loc. 33) the *Costistricklandia* Community was found in typical Wych Beds lithology a few feet above the highest sandstone. Higher horizons in the Wych Beds also yield the *Costistricklandia* Community at Gullet Quarry (Locs. 28, 29) and on the south side of Howler's Heath (Loc. 25). The *Clorinda* Community has been found at West Malvern (Loc. 31) indicating, as at Old Storridge Common, still deeper water in the upper part of the Wych Beds.

Correlation. At Gullet Quarry *Eocoelia curtisi* is present in the basal Wych Beds (Locs. 26, 27). This species is of C_5 age, as is *Costistricklandia lirata alpha* which occurs in higher beds at Gullet Quarry (Locs. 28, 29). The Cowleigh Park (Loc. 33), and West Malvern (Loc. 31) collections contain *C. lirata typica*, showing that, in the Malverns, the greater part of the Wych Beds is of C_6 age.

WOOLHOPE

Text-fig. 3, col. 26

Squirrel and Tucker (1960) proposed the names Lower Haugh Wood Beds and Upper Haugh Wood Beds for the Llandovery rocks exposed in the Woolhope dome, east-south-east of Hereford. The former are at least 280 ft. (90 m.) thick, their base unexposed, and are lithologically similar to the Wych Beds of the Malverns. The Upper Haugh Wood Beds are 30 ft. (10 m.) thick; the basal 20 ft. (7 m.) are purple and green muddy siltstones, but more calcareous beds are present in the top 10 ft. (3 m.).

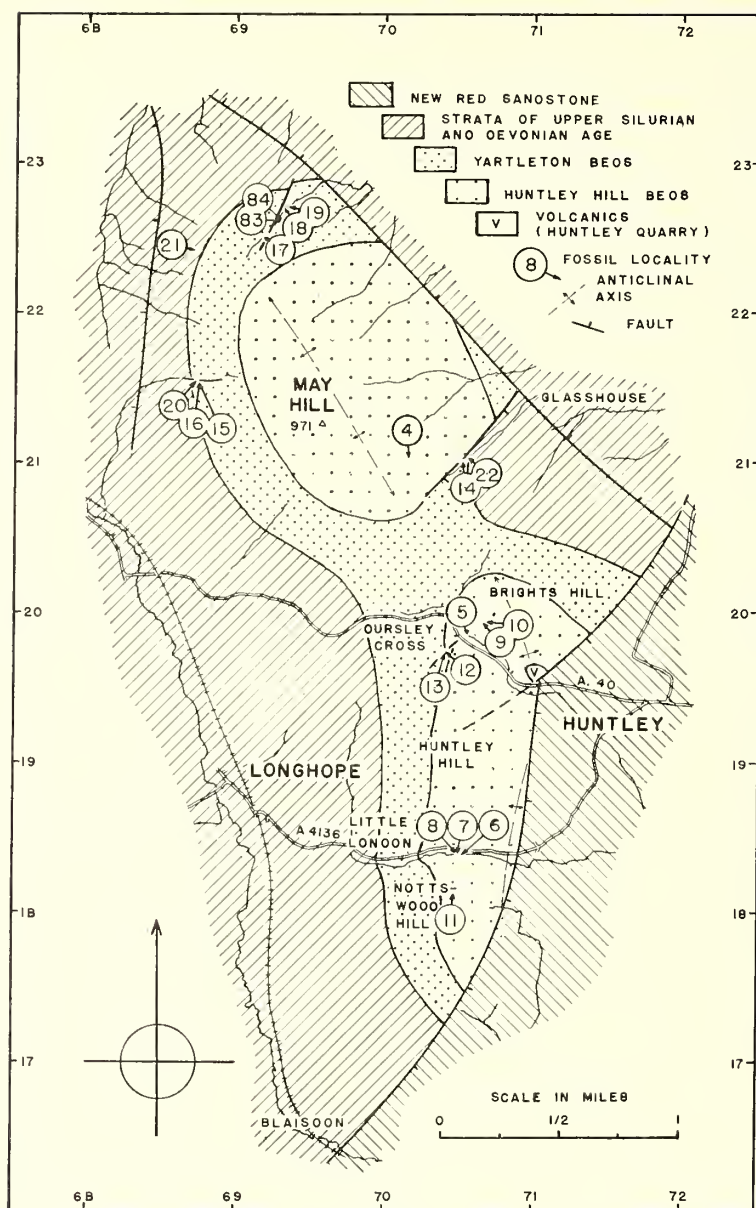
Fossil communities. In the Lower Haugh Wood Beds the *Costistricklandia* Community is represented by collections from Kidley Coppice (Loc. 85) and Rudge Wood (Loc. 86). Judging from the faunal lists of Squirrel and Tucker this community is also present in the Upper Haugh Wood Beds.

Correlation. *C. lirata typica* occurs in both the Lower and Upper Haugh Wood Beds, indicating a C_6 age. The *Petalocrius* Limestone is present in the highest 10 ft. (3 m.) of the Upper Haugh Wood Beds; it was found by Pocock (1930, pp. 60-1) at equivalent horizons in the May Hill and Malvern areas, but these exposures are now obscure. It is very close to the lithological boundary at the base of the Woolhope Limestone, and we conclude that this limestone is of late C_6 or early Wenlock age.

MAY HILL

Text-fig. 3, col. 27

Llandovery Beds are exposed in the core of an anticlinal structure at May Hill, 8 miles west of Gloucester (text-fig. 9). Two formation names, Huntley Hill Beds and



TEXT-FIG. 9. Locality map of the May Hill Inlier (after Lawson 1955, with minor changes).

Yartleton Beds, were proposed by Gardiner (1920) who also proposed the term Huntley Quarry Beds for 'Fine and somewhat coarse grits, containing lapilli' for beds in the vicinity of the quarry. At the present time, volcanic flows with interbedded red-beds are seen in Huntley Quarry, and these apparently underlie coarse sandstones with angular fragments of the volcanic rocks which grade up into fossiliferous Llandovery sediments.

The contact is obscure and faulted but it is probable that the Llandovery lies unconformably on these volcanics, which might possibly be correlated with similar volcanics in the Malvern Hills assigned to the Pre-Cambrian Warren House Series (Groom 1910). We regard the coarse grits in the vicinity, which have sometimes been included in the Huntley Quarry Beds, as the basal part of the Huntley Hill Beds, and propose the term Huntley Quarry Volcanics for the volcanic rocks and their associated red beds.

We also differ from the current literature concerning the relationship of the Yartleton Beds and the Woolhope Limestone. It has long been known (Phillips 1848, pp. 184–5) that a series of sandstones occur within the Woolhope Limestone sequence at Little London (SO/700 184) in the southern part of the inlier. Our mapping shows that the sandstone at Old Oaks Farm Quarry (Loc. 21) and the stream section near Hill Farm (Loc. 22) in the north-west and central parts of the inlier are also within the Woolhope sequence; in these two areas Lawson (1955) mistakenly referred these Woolhope sandstones to the Llandovery. Except for these minor points, we agree with Lawson's map of the Llandovery beds.

(a) *Huntley Hill Beds.* Lawson's (1955) minimum thickness of 600 ft. (200 m.) is probably an underestimate. The Little London stream section (SO/7085 1832 to SO/6997 1834) where the beds, with the exception of one outcrop, dip continuously to the west, suggests a thickness of about 850 ft. (280 m.). The oldest beds exposed in this section are on strike with the basal beds at Huntley Quarry, and are therefore near the base of the formation.

The Huntley Hill Beds are mostly grey coarse sandstones and conglomerates; they weather to a buff colour and are often reddened in areas close to the Triassic cover. The sandstone beds are normally one to 2 ft. thick; they show lateral changes in thickness, and they have little internal structure except towards the top of the formation where thinner bedded sandstones are present with fine parallel laminations. Shales are rare, but a few tens of feet of shale are exposed in the Little London stream (SO/7057 1837) at about 300 ft. above the base of the formation.

The pebbles in the conglomerates include the distinctive quartz-orthoclase plutonic rocks of the Malvern Hills. Volcanic pebbles are also present and could have been derived from other Malvern rocks or, in the case of the angular andesite prophyry pebbles, directly from the Huntley Quarry Volcanics. There is no doubt that adjacent pre-Cambrian rocks were being eroded at this time.

Fossil communities. The lowest 350 ft. (115 m.) of the Huntley Hill Beds are largely barren of fossils, but *Lingula pseudoparallela* has been reported from the basal sediments of Huntley Quarry (Symonds 1872, pp. 147–8). *Eocoelia hemisphaerica* and other representatives of the *Eocoelia* Community have been collected in the Little London stream section at about 350 ft. (Loc. 6) and 410 ft. (Loc. 7) above the supposed base of the formation; closely similar assemblages also occur near Dursley Cross (Loc. 5) and on the south-east side of May Hill (Loc. 4). At higher stratigraphical levels there is a reversion to the *Lingula* Community; about 440 ft. (140 m.) above the base in the Little London stream (Loc. 8), and in old quarries on Brights Hill (Locs. 9, 10). The highest Huntley Hill Beds are poorly exposed; a single fossil locality near old quarries at the top of Nottswood Hill (Loc. 11) has yielded the *Eocoelia* Community, with *E. intermedia* at about 610 ft. above the base of the formation.

Correlation. The lowest, largely unfossiliferous 350 ft. (115 m.) may be pre-Upper Llandovery in age. The beds between 350 and 410 ft. (115–35 m.) from the base of the formation in the Little London stream section are known to be of C_1 or C_2 age from the presence of *E. hemisphaerica*, as are the beds that have been correlated with these at Dursley Cross and May Hill. The Nottswood Hill quarries at around 610 ft. (200 m.) from the base contain *E. intermedia* of C_3 or C_4 age.

(b) *Yartleton Beds.* The lower contact of the Yartleton Beds is not exposed, but there appears to be a gradational transition from the coarse sandstones of the Huntley Hill Beds to the fine laminated sandstones (typically 3–4 in. thick), siltstones and shales of the Yartleton Beds. The formation is about 500 ft. (160 m.) thick.

Fossil communities. Fossil localities are abundant in the Yartleton Beds, but there are no well-exposed sections showing the stratigraphic relationships between exposures more than a few feet apart, as most of the outcrops occur along streams in the vicinity of faults. The fossil collections however can be arranged stratigraphically by comparing the *Eocoelia*, stricklandiids and pentamerinids with contemporaneous sections at Llandovery and in other parts of the Welsh Borderland. Table 1 summarizes the data for eleven localities at May Hill. The method used for calculating percentages is described in Ziegler, Cocks, and Bambach (1968, p. 4).

Except for the two collections (Locs. 18, 19) within 100 ft. (33 m.) of the Woolhope Limestone, all the Yartleton fossils belong either to the *Pentameroides* or *Costistricklandia* Communities or to mixtures of the two. Some changes in community composition apparently took place in a short period of time, for example, Locality 16, with 34% *Pentameroides* and 44% *Costistricklandia* contains elements of both communities but occurs a few inches above Locality 15 which consists of *Costistricklandia* with 8% *Clorinda*. Locality 16 may have a fauna from the boundary between the *Costistricklandia* and *Pentameroides* Communities, or it may be due to mixing of faunas after death. Locality 18 is interpreted as a death assemblage; it contains fairly abundant *Eocoelia* together with some deeper-water species. The highest locality in the Yartleton Beds, 19, is assigned to the *Clorinda* Community and represents deeper water than the earlier faunas.

Correlation. The majority of the Yartleton Beds are of C_5 and C_6 age (Table 1). It is possible that the basal parts are C_4 ; Locality 12 has no *Eocoelia* nor pentamerinids, and the stricklandiids are fragmentary and cannot definitely be assigned to *Stricklandia* or *Costistricklandia*, so it could represent an earlier horizon than the remaining collections.

At May Hill there is a transition between the Llandovery and Wenlock Beds. Phillips (1848, pp. 74–5, 184–5) arbitrarily drew the contact at the first appearance of limestone. Unfortunately the Woolhope Limestone and the overlying Wenlock Shales in the southern part of the Welsh Borderland have not yet yielded any graptolites that allow correlation with the graptolite zones and Phillips' arbitrary criterion must continue for the time being.

TORTWORTH

Text-fig. 3, cols. 28 and 29

Curtis (1955) has assigned the Llandovery rocks of this area (text-fig. 10) to two formations: the Damery Beds and the Tortworth Beds. These are separated by the 'Upper

Trap', an andesite flow with a fossiliferous ashy tuff bed on its upper surface (Reed and Reynolds 1908, p. 515, Reynolds 1924). The basaltic 'Lower Trap', considered intrusive by Reynolds (1924) but extrusive by Curtis, occurs at the base of the Damery Beds, resting unconformably on Tremadocian shales. Both basalts thin towards the north-west, and appear to be absent north of Stone.

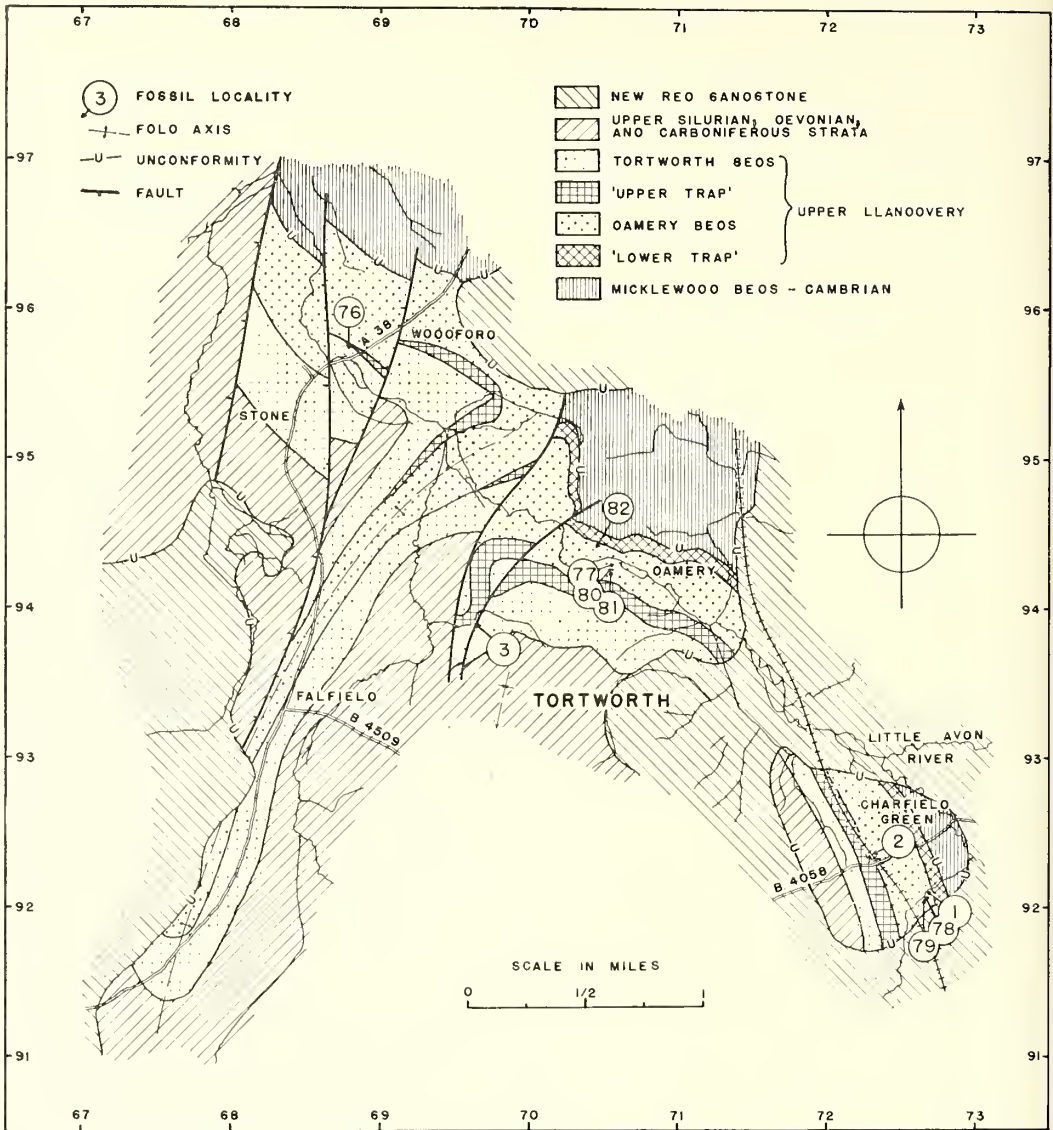
(a) *Damery Beds*. This unit is comprised of about 500 ft. (160 m.) of alternating fine-grained sandstone and shale beds (Curtis, 1955), with the former being dominant in the lower part of the unit.

TABLE 1. Critical community and dating elements of the collections from the Yartleton Beds (E, *Eocoelia*; P, *Pentameroides*; S, *Costistricklandia*; and C, *Clorinda*)

Section	Loc.	Community elements				Community	Dating elements	Date	Stratigraphical notes
		E	P	S	C				
Stream 450 yd. W. of Hay Farm (NE. side of May Hill)	19	7%	0%	3%	10%	C	<i>E. sulcata</i> <i>C. lirata typica</i>	C ₆	Within 100 ft. of Woolhope Lst.
	18	18	0	1	1	..	<i>E. sulcata</i> <i>C. lirata typica</i>	C ₆	Along strike from Loc. 19.
	84	3	0	8	1	S	<i>E. sulcata</i> <i>C. lirata typica</i>	C ₆	10 ft. above Loc. 83.
	83	12	18	26	0	P/S	<i>E. sulcata</i> <i>Pentameroides</i> sp. <i>C. lirata typica</i> <i>C. lirata alpha</i>	C ₆	(See above.)
	17	0	0	42	0	S	<i>E. sulcata</i> ? <i>C. lirata typica</i> <i>C. lirata alpha</i>	C ₅	
Stream S. of Pitman's Farm (W. side of May Hill)	20	4	0	4	0	S	<i>E. sulcata</i> ? <i>C. lirata typica</i> <i>Pentameroides</i> sp.	C ₆	
	16	0	34	44	0	P/S	<i>C. lirata alpha</i> <i>C. lirata alpha</i>	C ₅	A few inches above Loc. 15.
	15	0	0	29	8	S	<i>C. lirata alpha</i>	C ₅	(See above.)
Stream NW. of Hill Farm (SE. side of May Hill)	14	3	37	7	0	P	<i>E. curtisi</i> ? <i>Pentameroides</i> sp.	C ₅	
	13	3	34	19	0	P	<i>E. curtisi</i> ? <i>Pentameroides</i> sp.	C ₅	
Stream S. of Hollybush Farm, Dursley Cross	12	0	0	34	0	S		?C ₅	

Fossil Communities. The *Eocoelia* Community is present in the basal 130 ft. (43 m.) of the Damery Beds. Collections have been made within a few feet of the top of the Lower Trap in Damery Quarry (Loc. 82), and in higher beds at Charfield Green (Loc. 1) and near Damery Bridge (Loc. 77). The *Pentameroides* Community has been recognized in two collections, 10 ft. (3 m.) stratigraphically apart in the middle of the formation at Charfield Green (Locs. 78, 79). Still deeper water is indicated by the presence of the *Costistricklandia* Community in the top two-thirds of the Damery Beds; collections have been made on the road south of Damery Bridge at about 165 and 176 ft. (54–7 m.) above the base of the formation (Locs. 80, 81), and in the railway cutting at Charfield Green (Loc. 2) within 25 ft. (8 m.) of the top of the formation.

Correlation. *Eocoelia curtisi* occurs in all the collections from the lowest third of the Damery Beds, and *Costistricklandia lirata alpha* is present in the collections from the upper two-thirds of the formation. These show that all the Damery Beds are of C₅ age. The stream south of Charfield Green (Loc. 2) is the type locality of *E. curtisi* (Ziegler 1966b, p. 537).



TEXT-FIG. 10. Locality map of the Tortworth Inlier (after Curtis 1955).

(b) *Tortworth Beds*. The lithology of these beds is similar to the shales and fine-grained sandstones of the Damery Beds. Exposures are rare except near the base; Curtis (1955) estimates the thickness at 200 ft. (65 m.), but the upper contact appears to be gradational with an impersistent limestone forming the base of the Wenlock in the western parts of the Tortworth inlier.

Fossil communities. The only collections from the Tortworth Beds are from near the base. In Daniel's Wood (Loc. 3), the *Eocoelia* Community is present within a few feet

of the Upper Trap which is 150 ft. (50 m.) thick here; but north-east of Stone (Loc. 76) the *Costistricklandia* Community occurs in the basal foot of the Tortworth Beds where the basalt is only about 15 ft. (5 m.) thick. The different thicknesses of the lava appear to have controlled the local depth of water; *Costistricklandia* Community depths are present before and after the flow where it is thin, but where the flow is 150 ft. (50 m.) thick the deeper-water *Costistricklandia* Community at the top of the Damery Beds is replaced by the shallower-water *Eocoelia* Community above the andesite (Ziegler 1965).

Correlation. *Eocoelia sulcata* is present in both collections from the base of the Tortworth Beds; *Costistricklandia lirata alpha* is also present north-east of Stone (Loc. 76). The presence of *C. lirata alpha* and *E. sulcata* indicates that the horizon must be near the C₅-C₆ boundary.

WALSALL AND GREAT BARR

Text-fig. 3, col. 6

Butler (1937) has described Llandovery rocks in the Walsall Borehole, and Jukes (1853) and Eastwood *et al.* (1925, p. 11), mention a very small area of the Llandovery rocks at Great Barr near the Eastern Boundary Fault of the South Staffordshire Coalfield. The Walsall Borehole penetrated Wenlock Limestone, Wenlock Shale, Barr Limestone, and below this, some 457½ ft. (150 m.) of shales, mudstones, siltstones, and sandstones before hitting Cambrian quartzite with a dip differing by 8° to 15° from the Silurian. Some of the beds beneath the Barr Limestone are Wenlock in age as *Cyrtograptus murchisoni* has been recorded 36 ft. (12 m.) below this unit (depth 831½ ft.), but 74½ ft. (24 m.) below the Barr Limestone (depth 870 ft.) are purple and green shales, similar to the Hughley Shales of Shropshire, and we prefer to draw the Wenlock-Llandovery boundary at this point. Butler records 24 bentonitic clays above depth 870 ft., and 27 bentonites below this depth; one bed is 7 in. (18 cm.) thick, the remainder range from 2 in. down to ⅙ in. (5 cm.-1.5 mm.).

Fossil communities. The beds from 28 to 303 ft. (9.5-100 m.) above the base of the Silurian (depths 1225 to 950 ft.) contain *Costistricklandia*; in this sequence, *Pentameroides* (previously recorded as *Pentamerus oblongus*) is known only over a short thickness (233-48 ft. (76-81 m.) above base, or depths 1020 to 1005 ft.), so it appears probable that the Llandovery beds accumulated mainly in the moderate depths characteristic of the *Costistricklandia* Community. This interpretation agrees well with Butler's (1937, p. 251) picture of the depositional environment. The *Costistricklandia* Community also occurs at Great Barr where a Llandovery quartzite is exposed south-south-east of the house formerly known as the Australian Arms (SP/038957).

Correlation. *Costistricklandia lirata alpha* occurs between 28 and 93 ft. (9.5-31 m.) above the base of the sequence (depths 1225 to 1160 ft.) (Butler, 1937, p. 247), showing that the oldest Llandovery in this area is of C₅ age. *C. lirata typica* has been recorded between 123 and 283 ft. (41-93 m.) above the base (depths 1130 to 970 ft.), which proves a C₆ age for these beds. Graptolites occur at several horizons; those that Miss Elles examined from below 120 ft. (39 m.) from the base (depth 1133 ft.) are 'suggestive of the Upper Valentian', and those below 27 ft. (9 m.) from the base (depth 1226 ft.) suggest a horizon at least as low as the *M. griestoniensis* Zone (Butler 1937, p. 246). At the Great Barr exposure, we have collected *C. lirata typica*.

RUBERY

Text-fig. 3, col. 8

Llandovery rocks rest with slight angular unconformity on the Lickey Quartzite (Cambrian) to the north and south-east of Rubery (Wills *et al.* 1925, 1938, Eastwood *et al.* 1925, p. 12); the latter authors infer that it occurs in hollows in the quartzite. Wills *et al.* (1925, p. 68 and 1938, p. 177) describes the Rubery Shales Series as consisting of a minimum of 40–50 ft. (13–16 m.) of shales and thin sandstones with some calcareous beds; these rest on 100 ft. (33 m.) of Rubery Sandstone Series which are coarse and fine sandstones, some shale and a basal conglomerate.

Fossil communities. *Costistricklandia* is present in both the Rubery Sandstone series and the Rubery Shale Series; the faunal list of Wills *et al.* (1925, pp. 72–3) suggests that the *Costistricklandia* Community is present throughout the whole Llandovery sequence in this area, although *Pentameroides* does occur in some beds.

Correlation. *Costistricklandia lirata alpha* is abundant in the Rubery Sandstone Series (St. Joseph 1935, p. 419) and *Pentameroides* also occurs (previously recorded as *Pentamerus oblongus*). The higher Rubery Shale Series contains *C. lirata alpha*, *Monograptus marri* and *M. nudus*. It is concluded that the section described by Wills *et al.* (1925, p. 68) is all of C_5 age.

The fossils listed (Eastwood *et al.* 1925, pp. 14–15) as coming from Wenlock beds near Rubery Hill Asylum (SO/992778) include undoubted Llandovery fossils, but we have not examined this locality.

COVENTRY

Text-fig. 3, col. 9

Shotton (1927) records Upper Llandovery sandstone pebbles from the Corley Conglomerate of Upper Carboniferous age, which is exposed from Coventry to Corley and Hollyberry End (SP/262842) 6 miles to the north-west. Shotton has shown that, approaching Coventry from the north-west, the proportion of Llandovery sandstone pebbles increases from 46% at Hollyberry End, to 70% at Corley (SP/304850) and 85% at King Street, Coventry (SP/333797). This traverse along the present outcrop of the Corley Conglomerate runs obliquely to a south-south-eastward extension of the Nuneaton Ridge (composed of Cambrian and Precambrian rocks), and Shotton suggests (1927, p. 616) that this ridge was capped by a strip of Upper Llandovery rocks (as at Walsall and Rubery) which provided the pebbles. It is probable that the source area extended north-north-west from around Binley, 3 miles east of Coventry.

Fossil communities. The faunal list (Shotton 1927, pp. 609–10) contains 55 species, which, with one or two possible exceptions, are typical of, or known in, the *Eocoelia* Community. Stricklandiids, which are dominant to the west at Rubery and Walsall, are absent, as are *Pentameroides* and other elements of the offshore communities.

Correlation. Examination of *Eocoelia* in pebbles (some kindly lent from the Birmingham University collections by Professor Shotton, others in the Sedgwick Museum, Cambridge) show the present of *E. intermedia*, *E. curtisi*, and *E. sulcata*, which indicates

ages from C_{3-4} through C_5 to C_6 . This is the only record of Silurian beds as old as C_{3-4} to the east of the Malvern line.

LOWER LEMINGTON

Text-fig. 3, col. 20

Silurian rocks are recorded below Coal Measures in Strahan's (1913) description of a borehole 350 yd. W. 22° N. of Lower Lemington Church, 1 mile north-east of Moreton-in-Marsh. Grey shales with sandstone and limestone occurred from a depth of 1546 ft. (510 m.) to the completion of the hole at 1700 ft. (558 m.); allowing for a dip of 22° , the strata proved are about 140 ft. (46 m.) thick.

Fossil communities. Examination of the fossils in the Geological Survey collections (JP3143-61) from between 1590 and 1682 ft. show an *Eocoelia* Community present throughout this thickness.

Correlation. The *Eocoelia* present are all *E. sulcata*, indicating a C_6 age for all the fossiliferous Silurian beds that were penetrated.

EASTERN MENDIPS

Curtis (1955) summarizes the earlier work of Reynolds (1907, 1912, 1929) on the stratigraphy of the Silurian inlier which extends $3\frac{1}{2}$ miles westwards from Downhead, Somerset:

3. Wenlock mudstones with some micaceous sandstones (120 ft.—40 m.).
2. Andesites and tuffs (at least 400 ft.—130 m.).
1. Tuffs (110 ft. (36 m.) seen). These oldest beds have, in the past been assigned to the Upper Llandovery.

Fossil communities. A collection from a field 1 mile west of Downhead (Loc. 94) yielded a dominance of *Salopina* and *Sphaerirhynchia*, which suggest a near-shore environment for beds which our interpretation of the literature suggests are beneath the andesites.

Correlation. It is probable that there are no Llandovery beds exposed in the inlier. Collections from tuffs (ST6752 4584) suggest an environment similar to the *Eocoelia* Community of the Llandovery, but no *Eocoelia* or other distinctive Llandovery forms have been found by us or recorded in the literature. We have examined the specimens (GSM DEW 3833-935) upon which Green (1962) based his report of beds attributable to the Llandovery, and conclude that they are also of Wenlock or Ludlow age. We thus tentatively consider these beds to be of Wenlock age. This conclusion is supported by the presence of *Acaste downingiae* (Reynolds 1907, p. 227, Curtis 1955, p. 7) which we believe to be absent in the Llandovery.

RUMNEY

The Silurian inlier at Rumney (Rhymney), $2\frac{1}{2}$ miles north-east of the centre of Cardiff, has been described by Sollas (1879). The Silurian beds in this inlier have always been assigned to the Wenlock and Ludlow, although Sollas recorded *Pentamerus* and *Stricklandia*.

The problem has been investigated by Dr. M. G. Bassett, who kindly writes: 'I am certain that all the beds are Wenlock-Ludlow. The best exposure at present is at

Penylan Quarry, where virtually the oldest beds brought to the surface in the inlier are exposed. These beds are certainly below the Rumney Grit, and hence older than the horizons from which Sollas quoted his diagnostic Llandovery brachiopods. The beds at Penylan contain abundant *Meristina obtusa*, which I consider to be a good indicator of late Wenlock age. This is supported by the occurrence of other fossils which could only be Wenlock or Ludlow in age.' In addition there are many Wenlock brachiopods from the inlier at the National Museum of Wales which bear old labels mis-identifying them as '*P. oblongus*' and '*Stricklandia*'.

BREIDEN HILLS

Text-fig. 3, col. 4

Watts (1885, pp. 536–7) gave the first description of the Llandovery beds of the Breidden, and Wade (1911, p. 419) subdivided these beds into a lower unit, the Cefn Beds, and an upper unit, the Buttington Shales. The use of local names is preferable to the Shropshire names employed by Whittard (1932, pp. 880–2) in his description of this area. These beds are exposed sporadically along a 5-mile strip of country north-east of Buttington Station; the largest exposures are in the Brick Works (SJ/265 100) a quarter of a mile east of the station, and adjacent road sections.

(a) *Cefn Beds*. Whittard (1932) states that these consist of about 300 ft. (100 m.) of sandy mudstones with calcareous sandstones and occasional conglomeratic beds, but in the south-west the calcareous beds are more common. Ripples exposed at the top of the formation, over a large face in Buttington Brick Works, give a direction of movement from east to west.

Fossil communities. Whittard (1932, p. 881) mentions two fossil localities: north of Middletown in the centre of the outcrop (SJ/3008 1276) within 50 ft. (16 m.) of the base, and at the south-west end, south-east of Buttington Station (SJ/2633 0997) within 100 ft. (33 m.) of the base of the formation. Our collections show that the *Stricklandia* Community is present in both places.

Correlation. The presence of *Stricklandia lens* cf. *intermedia* suggests a Middle Llandovery age for the lower part of this formation.

(b) *Buttington Shales*. Whittard (1932, p. 881) described maroon, green, and blue mudstones with some calcareous beds up to 6 in. (15 cm.) thick, becoming uniformly maroon towards the top; he estimated their thickness to be about 350 ft. (115 m.). The upper contact is defined by an abrupt termination of the maroon coloured beds; above this Cocks and Rickards (in press) record the presence of a complete succession of Lower Wenlock graptolite zones at Buttington Brick Works.

Fossil communities. The Buttington Shales have few fossils, but we have a collection, from near the top of the sequence in the Brick Works, in the *Clorinda* Community. Whittard (1932, p. 882) also found fossils in loose blocks at the north-east end of the outcrop; his faunal list is also typical of the *Clorinda* Community.

Correlation. It is not possible to state what horizon within the Llandovery is represented by these two collections from the Buttington Shales, but they are overlain with apparent conformity by a basal Wenlock *centrifugus* Zone fauna.

WELSHPOOL

Text-fig. 3, col. 3

Wade (1911) described two formations of Llandovery age in the Welshpool area, the Powis Castle Beds and the higher Cloddiau Beds. The poorly exposed outcrop extends from Belan (2 miles south-west of Welshpool) to the Llansantffraid ym Mechain area, north-east of Meifod (see below).

(a) *Powis Castle Beds*. This unit consists of 100 ft. (33 m.) of massive bedded conglomerates; sandstones, shales and limestones are also present (Wade 1911, p. 431). It rests on Ashgill beds (*Phillipsinella parabola* age) in the Gwern y Brain (SJ/219 128) (Cave 1965, p. 282) and at the Laundry (SJ/197 103) (ibid., p. 295). Towards Welshpool the uppermost Ordovician beds are overstepped and the Powis Castle Beds rest on Lower Caradoc rocks (Harnagian Stage). In the Gwern y Brain, the Powis Castle Beds contain angular pebbles of these Ashgill and Caradoc units.

Fossil communities. A collection from the Gwern y Brain (SJ/2186 1283) within 10 or 15 ft. (3–5 m.) of the base of the Powis Castle Beds has yielded nothing but derived fossils from the underlying units, but the angularity of the pebbles and boulders is very suggestive of deposition in non-marine conditions. We have found the *Cryptothyrella* Community, a probable early Llandovery equivalent of the *Eocoelia* Community, in a loose block in the southern part of the area, 600 yd. west of Belan Locks (SJ/2100 0518). On Cherry Tree Bank (SJ/2226 0831) on the north edge of Welshpool, we have collected *Clorinda* from the higher beds of the unit, and this would suggest that some of the Powis Castle Beds accumulated in deeper water; this conclusion is strengthened by the presence of *Stricklandia lens* in the conglomerates in the north of Powis Castle Park. In fact, the full depth range of communities may be present in the formation.

Correlation. The fact that the overlying Cloddiau Beds contain a Lower Llandovery graptolite fauna (*vesiculosus* Zone) suggests that the Powis Castle Beds are of Lower Llandovery age, and suggests a short pause in sedimentation between the Ashgill beds in the Gwern y Brain and the earliest Silurian. The presence of *Stricklandia lens* indicates a Llandovery as opposed to a late Ordovician age for the unit.

(b) *Cloddiau Beds*. Around Welshpool, upper Silurian beds rest directly on the Powis Castle Beds, but from Cloddiau northwards, some 250 ft. (80 m.) of mudstones and siltstones are seen above the conglomerates.

Fossil communities. A collection from the Cloddiau Beds at Y Frochas (SJ/1955 0824) yielded the *Clorinda* Community.

Correlation. Wade (1911, p. 434) reported *Climacograptus innotatus*, *C. cf. rectangularis* and *C. medius* from the lower part of the formation near Cloddiau. These indicate the *vesiculosus* Zone, but as they were found only 20 ft. (7 m.) above the base of the formation, it is possible that the Middle and Upper Llandovery is also present—the Cloddiau Beds extent upwards into Wenlock strata with no change in dip.

MEIFOD

Text-fig. 3, col. 2

The Llandovery outcrop extends northwards from Welshpool for 7 miles to the Llansantffraid ym Mechain area (Whittington, 1938), and thence changes direction south-westwards to Meifod (King, 1928). King recognized four formations which he labelled V_1 , V_2 , V_3 , and VS and Whittington employed this terminology at Llansantffraid ym Mechain.

(a) *Craig-wen Sandstone* (V_1). This basal unit is a 30-ft. (10 m.) sandstone with some large calcareous concretions near the base. The sandstone fills hollows cut in Ashgill mudstone south-west and west of Meifod at Graig-wen and Glan-yr-afon-isaf (King 1928, pp. 682–3). These hollows are a foot or more in depth and contain angular fragments of Ashgill mudstone.

Fossil communities. King (1928, pp. 686–7, 699) records two communities from the Graig-wen Sandstone. In the calcareous beds fragmentary corals and brachiopods are present, while the sandstone contains 70% orthids, 20% *Cryptothyrella* (the *Meristina crassa* of earlier reports), and about 10% rhynchonelloids. Our collection from the basal 1½ ft. (50 cm.) of the unit at Graig-wen Quarry (SJ/0991 0919) has yielded the *Cryptothyrella* Community, the probable early Llandovery equivalent of the *Eocoelia* Community.

Correlation. The fossils of this unit are not diagnostic as to age, but the underlying Ashgill unit has yielded graptolites normally associated with the *Dicellograptus anceps* zone (King, 1928, p. 698) and the overlying formation has yielded late Lower Llandovery graptolites, so the Graig-wen Sandstone is probably of early Lower Llandovery age.

(b) *Blue silty mudstones* (V_2). Blue-black micaceous shales and hard siltstones (V_{2a}) come at the base of this formation west of Meifod; higher beds (V_{2b} and V_{2c}) in this 630-ft. (205 m.) formation are blue mudstones with silty siliceous bands and calcareous nodules (King 1928, pp. 687–8). Five miles north-east of Meifod, Whittington (1938, pp. 438–42) describes blue mudstones and limestones near Tre-wylan House and Gelli Farm (which he correlates with King's V_{2b} beds) resting on Ashgill. Similar beds occur at Godor and it would seem likely that the outcrop is continuous with that of Meifod. Beds like King's V_{2c} are recorded at Godor and Sarnau (Whittington 1938, pp. 440–1).

Fossil communities. King (1928, p. 699) lists *Stricklandia* and *Clorinda* [*Barrandella*] as common in V_{2b} ; and *Clorinda* as common in V_{2c} . This suggests deeper water than in the Graig-wen Sandstone.

Correlation. In the lower part of this unit, *Climacograptus normalis*, 'and what Dr. G. L. Elles thinks may be a specimen of *Monograptus acinaces*' have been found (King 1928, p. 688). These species would suggest the zone of *M. cyphus* (late Lower Llandovery), but the unit may extend into the Upper Llandovery as the lowest graptolite fauna in the overlying formation is in the *turriculatus* Zone.

(c) *Pale grey and purple-red shales* (V_3). King's (1928, p. 690) V_3 beds start with an abrupt change of colour from grey-blue mudstones to pale dove-grey fine mudstones; they consist of 330 ft. (110 m.) of pale grey and red shales.

Fossil communities. Apart from some fragmentary trilobites and brachiopods near the base, graptolites are the only fossils present.

Correlation. The zones present range from *turriculatus* to *crenulata* (King 1928, p. 690) and represent the upper two-thirds of the Upper Llandovery. The red shales occur in the *crispus* and *griestoniensis* Zones; they are the oldest dated red beds known in the Welsh Llandovery succession.

(d) *Passage Beds (VS).* King (1928, p. 691) records 60 ft. (20 m.) of blue-grey mudstones above V_3 beds.

Fossil communities. Benthic forms are absent from this unit.

Correlation. King found *Monoclinacis crenulata* in these beds to the north-east of Meifod, so they are assigned to the topmost Upper Llandovery. They are followed by lowest Wenlock beds with a similar lithology.

TRANNON AND LLANIDLOES

Text-fig. 3, cols. 1 and 10

These areas are in the middle of the graptolitic-greywacke facies of central Wales and have been included here because they contrast with the dominantly shelly facies of the Welsh Borderland areas already described. Wood (1906) and Jones (1945) have described the stratigraphy of the areas. At Trannon (called Tarannon by Wood) at least 3650 ft. (1200 m.) of Llandovery sediments (we use Llandovery to include all the beds up to the base of Wood's *murchisoni* Zone) are present, and 9670 ft. (3175 m.) at Llanidloes. In both areas the whole succession consists of graptolitic shales with greywackes at some horizons. The base of the Silurian is not quite reached near Trannon, but at Llanidloes a sharp but comfortable base is present.

Greywackes are especially abundant in the *griestoniensis* Zone. Bassett (1963, pp. 57-9) interprets the Talerddig Grits of Trannon and the contemporary Moelfre Group of Llanidloes as turbidites and comments on the problems in estimating the depth of water in which they were deposited. We would consider that these turbidites could have been laid down over a very large depth range, provided that the depth was greater than that of the *Clorinda* Community, which is completely absent around Trannon.

The highest Llandovery consists of purple and green mudstones which contain a fauna characteristic of the *crenulata* Zone. There is a gradational passage upwards into the Wenlock beds.

BUILTH WELLS

Text-fig. 3, col. 23

Upper Llandovery rocks occur in a very narrow discontinuous belt running north-east from Park Wells (SO/027 519—1 mile west-north-west of Builth Wells) for a distance of 4 miles (Jones 1947). The beds consist of about 50 ft. (16 m.) of coarse sandstone and mudstones, resting unconformably on Ordovician beds, and overlain unconformably by beds of Lower Wenlock age. The Wenlock overstep is considered to be responsible for the discontinuous outcrops (Jones 1947, p. 35).

Fossil communities. A collection from Trecoed (SO/0527 5516) has yielded an abundance

of *Pentamerus* and *Stricklandia*, suggesting a mixture of these two communities. These came from a coarse sandstone about 14 ft. (5 m.) above the base of the Llandovery.

Correlation. *S. lens ultima* is present, indicating a C₃₋₄ age for this horizon.

GARTH

Text-fig. 3, cols. 21 and 22

The Garth area is situated some 15 miles north-east of Llandovery and is part of the same belt, which, during Llandovery times, formed the junction of the stable shelf to the south and east and the subsiding basin to the north and west. The two columns representing this area were selected to illustrate some of the many lateral changes in thickness and lithology in the Llandovery rocks of the Garth area. Andrew (1925) divided the Lower Llandovery into three formations, A_a, A_b, and A_c; designated the Middle Llandovery B; and divided the Upper Llandovery into C_a, C_b, C_c, and C_d.

(a) *Lower Llandovery.* The basal Llandovery sandstones and conglomerates rest on Bala mudstones with a sharp boundary; these are followed by mudstones with occasional sandy beds, all totalling 1880 ft. (600 m.) in the centre of the area, but thinning to 1200 ft. (400 m.) in the south-west (Andrew 1925, pp. 392, 402).

Fossil communities. No fossils are recorded in A_a. In the southern part of the area, the *Stricklandia* Community is present in A_b, and both *Stricklandia* and *Clorinda* occur in A_c, but the shelly faunas become sparse or absent in the north (Andrew 1925, pp. 396-7), that is, towards the basin.

Correlation. Andrew (1925, p. 403) considered 'on faunal and lithological grounds': that his units 'A_a, A_b, and A_c appear accurately to represent A₁, A₂, and A₃ of the southern part of the Llandovery area'. It is of importance to note that the top 20 ft. of the 'Bala' beds of Garth contain '*Glyptograptus* cf. *persculptus* and *Mesograptus* cf. *modestus* var. *parvulus*, which . . . are usually associated with the basal zone of the Valentian' (Andrew 1925, p. 392). This fauna indicates the *persculptus* Zone, the base of which is now conventionally taken (e.g. Toghil 1968) as the base of the Llandovery in the graptolite sequence. If Andrew was correct in equating his unit A_a with the A₁ sandstone at Llandovery itself, then the base of the formation is probably diachronous. The latter conclusion is supported by recent unpublished sedimentological work by Dr. M. A. Woollands.

(b) *Middle Llandovery.* Only a small thickness of mudstones is present in a restricted area in the south-east of the Garth area (Andrew 1925, p. 397). The few specimens recorded are suggestive of the *Clorinda* Community. Andrew suggested a correlation with B₃ of Llandovery on the basis of lithological resemblance (Andrew 1925, p. 403), but its age is still not definitively known.

(c) *Upper Llandovery.* The lower three Upper Llandovery units of Andrew (C_a, C_b, C_c) comprise a sequence of mudstones, argillaceous sandstones, and rather prominent conglomerates which is very variable in thickness (0-300 ft., 0-100 m.). The upper unit (C_d) consists of 150-1000 ft. (50-330 m.) of olive-green and purple mudstones, similar in colour and lithology to the high Llandovery of many other areas; it overlaps earlier

beds, coming to rest on A_b at the extreme south-western and north-eastern ends of the area, according to the mapping of Andrew. C_d passes up without a break into beds containing the basal Wenlock zone of *Cyrtograptus purchisoni* (Andrew 1925, p. 400).

Fossil communities. Andrew's faunal lists (1925, pp. 398-9) show that C_a contains a *Pentamerus* Community, which indicates a shallowing after the Middle Llandovery. C_b has yielded a fauna which includes *Pentamerus*, *Stricklandia*, and *Clorinda*, suggesting a return to deeper water. It is not possible to determine the community present in C_c , but increase in depth is again shown by the graptolites present in C_d .

Correlation. The Upper Llandovery of Garth can be tentatively correlated with the beds of Llandovery on gross lithological and faunal grounds. Andrew and Jones (1925, p. 412) suggest it may be equivalent to C_{4-6} . The presence of beds with *Monograptus priodon* and *Monoclinacis cremulata* conformably below the basal Wenlock shows that the highest Llandovery is present in this area.

CHRONOLOGICAL SUMMARY

Text-fig. 11 illustrates the chronological sequence of Llandovery deposits in the Welsh Borderland. It brings out the fact that, although the spread of the sea was continuous from Lower Llandovery times, there were several gaps in sedimentation. In general, however, there is evidence of a progressive deepening at any one locality.

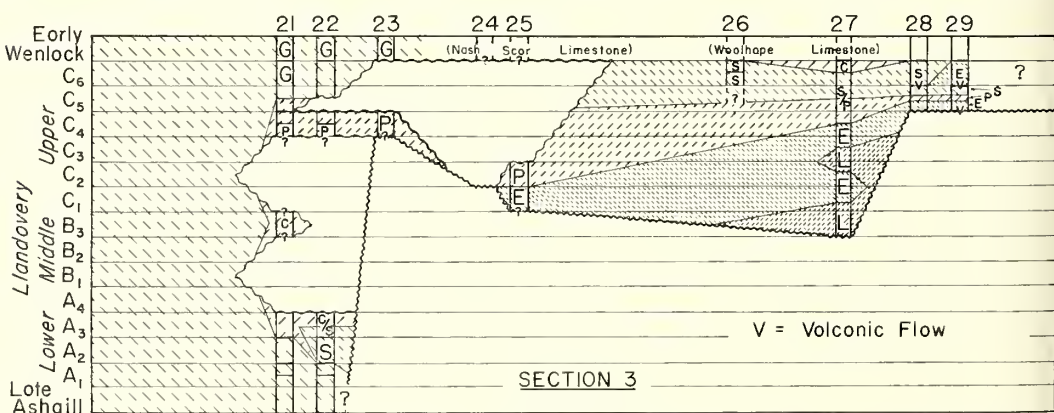
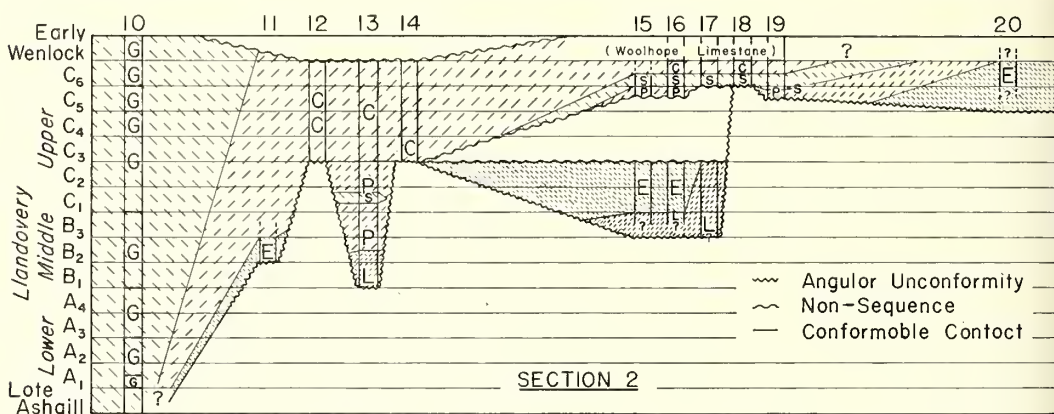
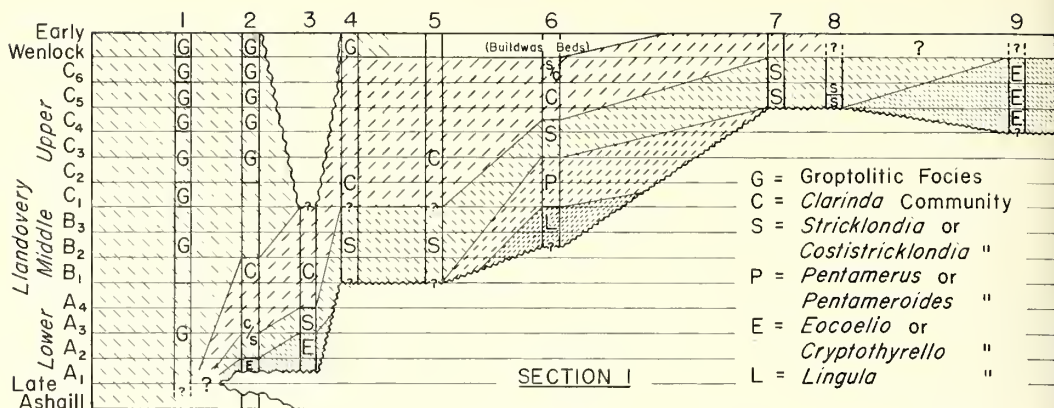
Lower Llandovery (A_{1-4}) times

The shelf was narrow during the Lower Llandovery, and deposits are confined to an area west of Welshpool and Garth (text-fig. 12). In the basin area of Central Wales (text-fig. 11, cols. 1, 10, 21, and 22), basal Llandovery graptolitic shales follow above similar Ashgill sediments without a break. At Trannon and Llanidloes this facies continues throughout the Lower Llandovery, but at Garth *Stricklandia* and *Clorinda* Communities are present, showing that shallowing took place there in A_{2-3} times. This was probably followed by a depositional break, as no A_4 has been proved at Garth.

On the edge of the basin at Meifod and Welshpool (text-fig. 11, cols. 2 and 3), there was uplift of Ashgill sediments prior to the deposition of beds containing A_{1-2} shallow-water *Cryptothyrella* Communities. In Shropshire, to the east (text-fig. 11, cols. 5, 6, 11-14), the Caradoc and earlier rocks are seen to be considerably folded before the Middle Llandovery. If these movements are correlated with the basal A_1 non-sequence at Meifod and Welshpool, then it may be that the acme of this folding occurred at the very beginning of the Silurian. After the initial uplift, the shallow-water A_{1-2} beds at Meifod and Welshpool are followed by deeper-water A_3 *Stricklandia* and *Clorinda* Communities. The general subsidence characteristic of the Welsh Borderland throughout the Lower Silurian thus started as early as A_{2-3} times.

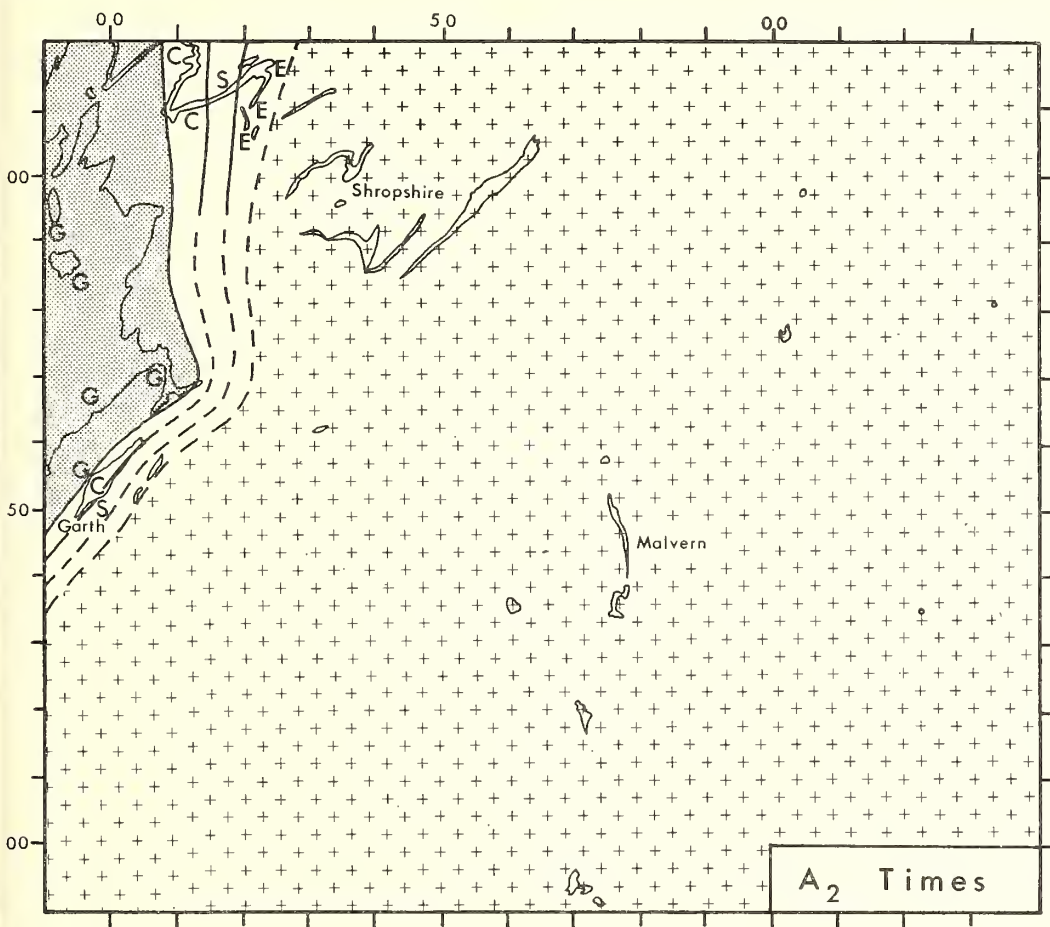
Middle Llandovery (B_{1-3}) times

In the basin (text-fig. 11, cols. 1 and 10), the graptolitic facies continues without break; this facies spread over the basin margin at Meifod (text-fig. 11, col. 2) in B_2 time, when the *Clorinda* Community was replaced by graptolites. At about the same time, the sea



TEXT-FIG. 11. Three sections across the Welsh Borderland (see text-fig. 1 and 3) showing communities plotted against time.

deepened at Welshpool (text-fig. 11, col. 3) and spread over West Shropshire (text-fig. 11, cols. 4, 5, 11, and 13) and may have just reached the Malverns (text-fig. 11, cols. 15-17) by the end of Middle Llandovery times. It is worth noting here that there are no Middle Llandovery sediments in nearby sections at Eaton Farm and Wistanstow



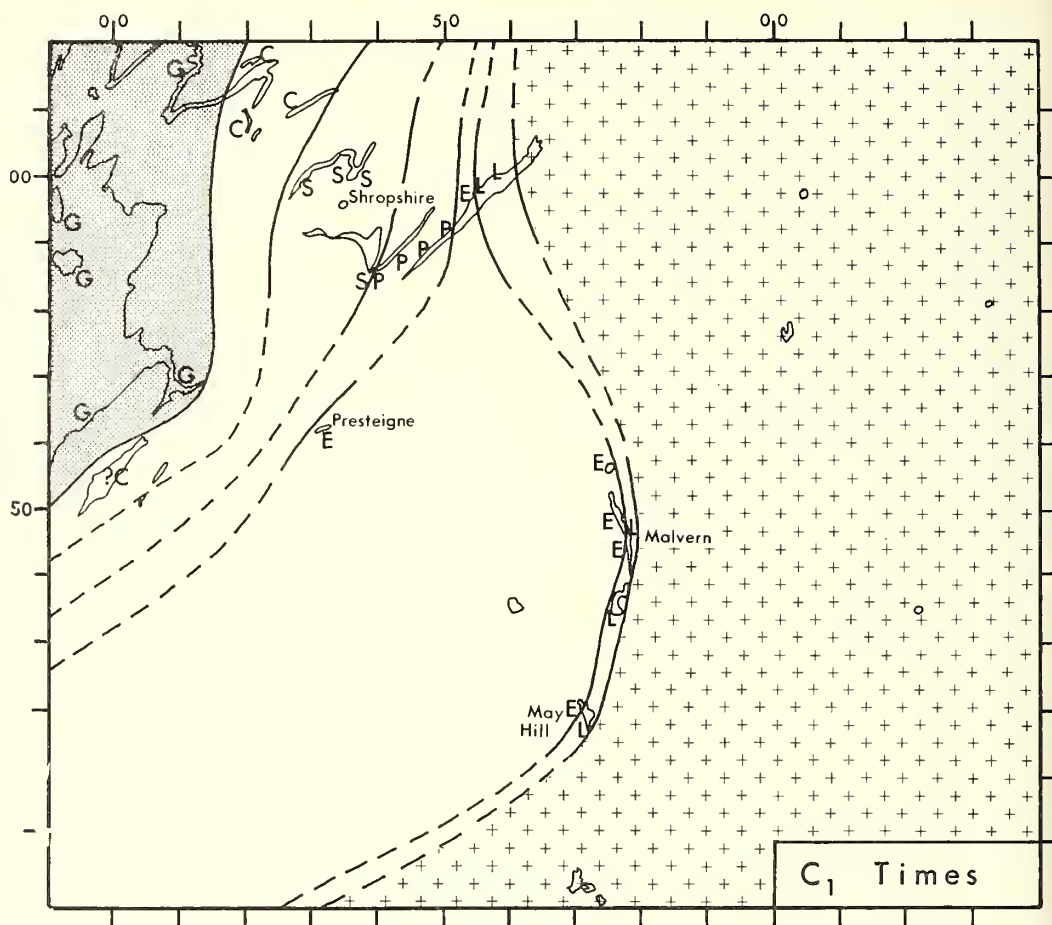
TEXT-FIG. 12. Palaeogeography of the area during Lower Llandovery (A_2) time. E, *Cryptothyrella* Community; S, *Stricklandia* Community; C, *Clorinda* Community; G, graptolitic facies.

Note. The coastline is shown as a smooth curve, but we envisage a coastal topography perhaps similar to Essex at the present time (this applies also to text-fig. 13 and 14). The size of some of the smaller outcrops is enlarged for greater clarity, and the Upper Severn Estuary is omitted.

(text-fig. 11, cols. 12 and 14). The earliest deposits at these localities contain C_{2-3} *Clorinda* Communities; this shows that the sea was deep before sedimentation commenced, and that the advance of the sea was not everywhere accompanied by a supply of sediments. Thus the sea probably extended over the Eaton Farm and Wistanstow areas in Middle Llandovery time.

Early Upper Llandovery (C₁₋₃) times

At Trannon, Meifod, and Llanidloes (text-fig. 11, cols. 1, 2, and 10) the graptolite facies continues, both in the basin and on the edge of the shelf (text-fig. 13). In West Shropshire (text-fig. 11, cols. 4 and 5) the sea is seen to have deepened with the replace-

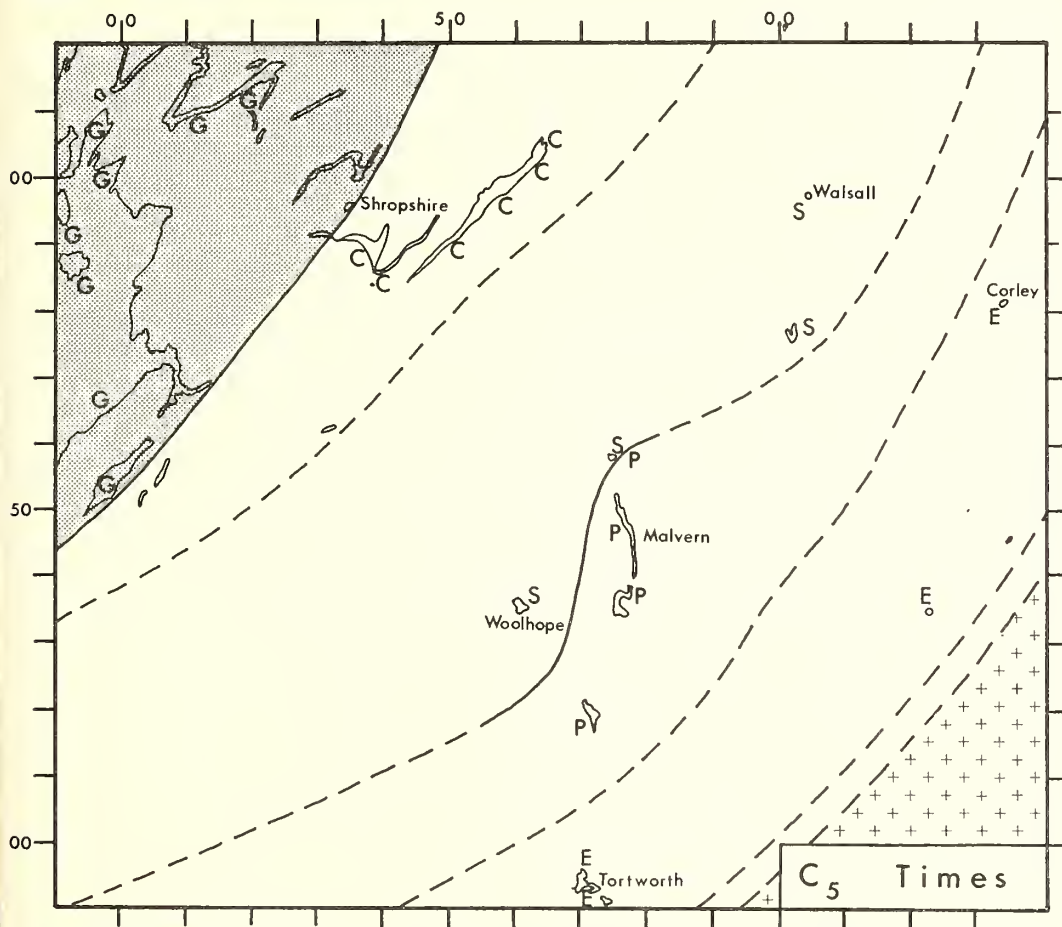


TEXT-FIG. 13. Palaeogeography of the area during early Upper Llandovery (C₁) time. L, *Lingula* Community; E, *Eocoelia* Community; P, *Pentamerus* Community; S, *Stricklandia* Community; C, *Clorinda* Community; G, graptolitic facies.

ment of the *Stricklandia* Community by the *Clorinda* Community. South of the Longmynd (text-fig. 11, col. 13) the communities show a minor reversal, but there was an over-all deepening from C₁ to C₃ times. At neighbouring sites (text-fig. 11, cols. 12 and 14) sedimentation commenced for the first time with the deposition of deep-water *Clorinda* Communities resting directly on Pre-Cambrian and Ordovician rocks.

In the Wenlock Edge outcrop, and in the Malverns and at Presteigne (text-fig. 11, cols. 6, 15-17, and 25), there are undoubted early Upper Llandovery sediments; these contain shallow-water communities showing the progressive deepening so characteristic

of this transgression. There is a sequence from a basal *Lingula* Community (not exposed at Presteigne) deepening to *Eocoelia* or *Pentamerus* Communities. At May Hill (text-fig. 11, col. 27) there is a minor reversal in the progressive deepening as *Lingula* and *Eocoelia* Communities alternate.



TEXT-FIG. 14. Palaeogeography of the area during late Upper Llandovery (C_5) time. E, *Eocoelia* Community; P, *Pentameroides* Community; S, *Costistricklandia* Community; C, *Clorinda* Community; G, graptolitic facies.

At Garth and Builth (text-fig. 11, cols. 21–3) no beds of C_{1-3} age are present, this is probably to be accounted for by non-deposition in a sea of *Pentamerus* Community depth, as this community is present above the non-sequence in beds of C_4 age.

Late Upper Llandovery (C_{4-6}) times

During this time, basin facies (the Pale Shales) continue at Garth (text-fig. 11, col. 21), but, in Wenlock times, graptolitic deposits are present at Builth as well (col. 23); an eastwards spread of this deep environment thus presumably occurred in C_6 times (text-fig. 14). A similar C_6 spread probably took place over the edge of the basin from

Montgomeryshire into West Shropshire (text-fig. 11, cols. 2-4); this deepening of the sea may also be related to the turbidities at Minsterley (which are of late Upper Llandovery [post C_4] or early Wenlock [pre-*riccartonensis* Zone] age).

On Wenlock Edge (text-fig. 11, col. 6), the progressive deepening, mentioned above, continues through most of C_{4-6} , but in late C_6 time there is an indication of slight shallowing in the beds immediately below the Buildwas Beds.

From sandstone pebbles in the Upper Carboniferous north-east of Coventry (text-fig. 11, col. 9), *Eocoelia* has been found, ranging in age from C_4 to C_6 . However, at Walsall and Rubery (text-fig. 11, cols. 7 and 8) the earliest Silurian deposits contain C_5 beds with *Costistricklandia* Communities and rest directly on Cambrian rocks; here, as in Shropshire during C_{1-3} (see above), we have strong indications that the sea was present at Walsall and Rubery well before sedimentation commenced. The evidence from Lower Lemington (text-fig. 11, col. 20) suggests a shallow sea there in C_6 times, but the local base of the Silurian is unseen.

In the Malvern areas (text-fig. 11, cols. 15-19), no beds of C_{3-4} age are known; this non-sequence is followed by C_5 beds with *Pentameroides* and *Costistricklandia* Communities which overlap the C_{1-2} deposits (which contain *Lingula* and *Eocoelia* Communities), and rest in places on the Pre-Cambrian. Text-fig. 11 shows that there is a progressive deepening of the sea across this non-sequence; thus there is no suggestion of any marine regression during C_{3-4} time in the Malvern area.

A different type of stratigraphical break is present beneath the Nash Scar Limestone at Presteigne and Old Radnor (text-fig. 11, cols. 24 and 25); a shallow-water Wenlock algal limestone rests unconformably on C_2 beds (with a *Pentamerus* Community) at Presteigne, and on Pre-Cambrian at Old Radnor. There must have been shallowing during this interval, and local uplift may well have occurred here during the late Upper Llandovery.

The progressive deepening, seen or inferred for C_{4-6} beds of most areas, was also present to the south of the Malverns in the May Hill and Tortworth areas (text-fig. 11, cols. 27-9). At May Hill the communities range from *Eocoelia* through *Pentameroides* and *Costistricklandia* to *Clorinda*, and at Tortworth the Stone succession (col. 28) also shows a progressive sequence. This last sequence contains a 15-ft. (5-m.) thick basalt within the beds containing the C_6 *Costistricklandia* Community. But at the other end of the Tortworth Inlier (at Charfield Green, text-fig. 11, col. 29) the basalt has thickened to 150 ft. (50 m.), and is followed directly by beds containing an *Eocoelia* Community. We conclude that the sudden shallowing of the shelf sea by 150 ft. is directly responsible for the replacement of a *Costistricklandia* Community by an *Eocoelia* Community; this implies that the depth range of the intervening *Pentameroides* Community is significantly less than 150 ft.

CONCLUSIONS

The elucidation of the evolution of several brachiopod genera has enabled wide correlation of the 13 subdivisions of the Llandovery established in the type area by O. T. Jones. Recognition of similar assemblages of fossils at different times has led to the establishment of five main animal communities. In the Silurian the marine communities of the shelf were largely epifaunal and relatively independant of substrate; depth was thus the main controlling factor in community distribution.

In the shelf regions on the Welsh Borderland, the Llandovery always rests unconformably on older rocks; on the margin of the basin there is only a small break at the very base of the Lower Llandovery; and in the basin of Central Wales there is conformity between the Ordovician and Silurian. From A_1 to C_6 there was a progressive spread of the sea to the east and south. In the Lower Llandovery marine deposits are present at Welshpool and Garth; by Middle Llandovery times West Shropshire had been submerged; and by early Upper Llandovery (C_1) times the sea had transgressed as far as the Malverns and May Hill; it did not reach Tortworth until the late Upper Llandovery (C_5). The theory (Jones 1938) that there was a sudden submergence of the whole area at the beginning of the Upper Llandovery cannot now be accepted.

With few exceptions, each local sequence shows a progressive increase of depth with time. This progressive depth increase can even span periods of non-deposition, for example the C_5 beds above the non-sequence in the Malverns were laid down in deeper water than in C_2 beds below the break. We have concluded that, where a deeper-water community is present at the base of a local sequence, the sea was present for some time before deposition commenced. It follows that the spread of the sea with time was even more uniform than the sedimentary sequences record. It also follows that there were periods when no sediments were being deposited in certain parts of the sea floor; this may have been due either to lack of sediment supply or to no deposition or erosion in current-swept areas.

The Welsh Borderland is on the south-eastern margin of a Lower Palaeozoic geosyncline which included the Lake District, the Southern Uplands of Scotland and much of central Ireland. Both this margin and the western margin in County Galway show an extension of the sea during Llandovery times, but at the same time north-east Newfoundland (and perhaps also parts of the Midland Valley of Scotland, for example, Lesmahagow), show a transition from deep-water basin sediments to shelf or even non-marine conditions. When the Welsh Borderland is viewed as part of this larger region, it seems improbable that the advance of the sea during Llandovery times was due to eustatic deepening.

Although there was probably little structural control of sedimentation from place to place within the Welsh Borderland at this time, there were three major tectonic regions affecting the area:

- (i) The basin region to the west which subsided rapidly, accommodating large thicknesses of sediment (nearly 10 000 ft. (3300 m.) of Llandovery beds at Llanidloes).
- (ii) The shelf region, which subsided slowly throughout the whole of Llandovery time, and upon which thinner sediments accumulated.
- (iii) A region of uplands to the south and east, which provided the sediment for both of the other regions.

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APPENDIX 1

Localities of collections in Oxford University Museum

<i>Area</i>	<i>Locality</i>	<i>Field designation</i>	<i>Grid reference</i>
Tortworth	1	T-M-A	(ST/7268 9212)
	2	T-R-A	(ST/7233 9234)
	3	T-D-A	(ST/6962 9390)
May Hill	4	M-N-A	(SO/7014 2104)*
	5	M-D-A	(SO/7055 1987)
	6	M-L-A	(SO/7052 1838)
	7	M-L-B	(SO/7049 1838)
	8	M-L-C	(SO/7048 1839)
	9	M-Q-A	(SO/7066 1994)
	10	M-Q-B	(SO/7067 1993)
	11	M-H-A	(SO/7047 1811)
	12	M-B-A	(SO/7041 1974)
	13	M-B-B	(SO/7039 1973)
	14	M-G-C	(SO/7051 2097)
	15	M-F-D	(SO/6874 2154)
	16	M-F-A	(SO/6874 2154)
	17	M-S-A	(SO/6918 2261)
	18	M-S-B	(SO/6932 2270)
	19	M-S-C	(SO/6936 2271)
	20	M-F-C	(SO/6872 2155)
	21	M-O-A	(SO/6869 2244)
	22	M-G-B	(SO/7055 2103)
Malvern Hills	23	H-O-A	(SO/7533 3764)
	24	H-H-A	(SO/7487 3595)
	25	H-T-A	(SO/7494 3492)
	26	H-G-A	(SO/7612 3811)
	27	H-G-D	(SO/7612 3811)
	28	H-G-E	(SO/7612 3811)
	29	H-G-F	(SO/7608 3811)
	30	H-P-A	(SO/7646 4594)
	31	H-C-A	(SO/7672 4442)
	32	H-R-A	(SO/7613 4784)
	33	H-S-A	(SO/7616 4723)
Old Storridge Common	34	H-L-A	(SO/7467 5115)
	35	H-F-C	(SO/7444 5124)
	36	H-M-A	(SO/7430 5152)
	37	H-M-B	(SO/7430 5152)
	38	H-L-C	(SO/7464 5108)
	39	H-L-B	(SO/7464 5111)
	40	H-F-B	(SO/7438 5114)
	41	H-M-C	(SO/7405 5167)
Ankerdine Hill	42	A-A-A	(SO/7352 5625)
	43	A-H-A	(SO/7376 5696)
	44	A-Q-A	(SO/7363 5630)
	45	A-K-A	(SO/7347 5690)

* Collections from loose blocks.

<i>Area</i>	<i>Locality</i>	<i>Field designation</i>	<i>Grid reference</i>
Wenlock Edge	46	Morrellswood	(SJ/6284 0637)
	47	Boathouse A	(SJ/6210 0379)
	48	Boathouse B	(SJ/6206 0390)
	49	Boathouse C	(SJ/6205 0398)
	51	Sheinton B	(SJ/6116 0310)
	52	Merrishaw A1	(SJ/5805 0090)
	53	Merrishaw A2	(SJ/5805 0090)
	54	Merrishaw B	(SJ/5852 0065)
	55	Domas	(SJ/5936 0062)
	56	Hughley	(SO/5605 9747)
	58	Wall-u-Heywood	(SO/5120 9276)
	59	Ticklerton	(SO/4821 9088)
	60	Onny River	(SO/4260 8532)
Church Stretton	61	Marshbrook	(SO/4341 8982)
	62	Hillend Farm	(SO/3956 8769)
Norbury	63	Norbury	(SO/3587 9284)
Bog	65	Bog A	(SO/3510 9815)*
	66	Bog B	(SO/3510 9815)*
Minsterley	67	Ox Wood Dingle	(SJ/2909 0123)
	68	Venusbank	(SJ/3534 0125)
	69	Hope Outlier	(SJ/3482 0140)
	70	Hope Quarry	(SJ/3551 0208)
	71	Hope Brook	(SJ/3578 0212)
	72	Josey's Wood A	(SJ/3656 0213)
	73	Josey's Wood B	(SJ/3653 0221)

APPENDIX 2

Localities of collections in British Museum (Natural History)

<i>Area</i>	<i>Locality</i>	<i>Field designation</i>	<i>Grid reference</i>
Wenlock Edge	50	Sheinton A	(SJ/6099 0324)
	57	Gilberries	(SO/5115 9361)
Norbury	64	Linley Wall	(SO/3587 9284)*
Minsterley	74	Josey's Wood C	(SJ/3641 0216)
	75	Minsterley Lane	(SJ/3803 0487)

APPENDIX 3

Localities of collections in United States National Museum

<i>Area</i>	<i>Locality</i>	<i>U.S.N.M. no.</i>	<i>Grid reference</i>
Tortworth	76	10215	(ST/6879 9574)
	77	10217	(ST/7056 9428)
	78	10218	(ST/7267 9206)
	79	10219	(ST/7267 9206)
	80	10220	(ST/7055 9426)
	81	10221	(ST/7055 9426)
	82	10223	(ST/7045 9440)*

* Collections from loose blocks.

<i>Area</i>	<i>Locality</i>	<i>U.S.N.M. no.</i>	<i>Grid reference</i>
May Hill	83	10225	(SO/6927 2263)
	84	10226	(SO/6927 2263)
Woolhope	85	10230	(SO/5804 3730)
	86	10232	(SO/5948 3564)
Old Storridge Common	87	10237	(SO/7496 5156)
Presteigne	88	10242	(SO/3177 6343)
	89	10243	(SO/3197 6334)
	90	10244	(SO/3160 6320)
	91	10245	(SO/3153 6316)
	92	10246	(SO/3155 6317)
	93	10247	(SO/3018 6235)
Eastern Mendips	94	12936	(ST/6755 4585)*

* Collections from loose blocks.

A. M. ZIEGLER

Department of the Geophysical Sciences
University of Chicago
Illinois 60637, U.S.A.

L. R. M. COCKS

Department of Palaeontology
British Museum (Natural History)
London S.W. 7

W. S. MCKERROW

Department of Geology and Mineralogy
Parks Road
Oxford

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THE UNUSUAL BRACHIAL SKELETON OF *ATTENUATELLA CONVEXA* SP. NOV. (BRACHIOPODA)

by JOHN ARMSTRONG

ABSTRACT. Excellently preserved specimens of *Attenuatella convexa* sp. nov. have enabled reconstruction of a unique brachial skeleton for *Attenuatella*. Apart from this characteristic the genus is closest to members of the Ambocoeliinae (Spiriferida) and its inclusion in this subfamily is still the most plausible supra-generic grouping. Globally, eleven species of *Attenuatella* are now documented and the known range of the genus is from the lower Artinskian (Aktastinian) to the Kazanian or Wordian Stage. The species *Attenuatella convexa* sp. nov., *Attenuatella* sp. A, and *Attenuatella* sp. cf. *incurvata* Waterhouse are here described from Queensland.

ATTENUATELLA STEHLI (1954) is a small, very distinctive spiriferid which occurs at only a few localities throughout the world. The genus has recently been documented from Australia by Waterhouse (1967) and by Armstrong and Brown (1968) who describe species from New South Wales and Queensland respectively. Several additional occurrences are known from the Permian faunas of Queensland and the species from these are described here. Serial acetate peels of well-preserved specimens of one of these species, *Attenuatella convexa* sp. nov., have supplemented the hitherto only fragmentary information that is available about the brachial skeleton of the genus.

Specimens of *Attenuatella* from a number of the localities in Queensland were kindly lent by Dr. J. M. Dickins of the Bureau of Mineral Resources, by Dr. J. F. Dear of the Geological Survey of Queensland, and by Dr. B. N. Runnegar of the University of Queensland. Dr. Dickins made available specimens which he collected from three localities in the Bowen Basin, and Dr. Dear and Dr. Runnegar each supplied a specimen which they had collected from the Barfield Formation in the Bowen Basin, and from just below the Upper Limestone near Gympie respectively. Bureau of Mineral Resources localities referred to, occur on the Duaringa and Taroom 1:250,000 military maps and are designated by a number prefixed by Du and T respectively. Geological Survey of Queensland, and University of Queensland Department of Geology and Mineralogy locality numbers are prefixed by GSQL and UQL respectively. All specimens mentioned have individual numbers which follow the initials of the institution in which the specimens are housed; CPC, Commonwealth palaeontological type collection, Bureau of Mineral Resources, Canberra; GSQF, Geological Survey of Queensland; UQF, Department of Geology and Mineralogy, University of Queensland.

Order SPIRIFERIDA Waagen 1883
Subfamily AMBOCOELIINAE George 1931

Remarks. The brachidia of *Attenuatella* are unusual and are very distinctive. Serial acetate peels prepared from ten specimens of *Attenuatella convexa* sp. nov. do not show any traces of spiralia but they reveal the structures shown in text-fig. 1. Waterhouse (1964) has also figured serial sections of specimens of a species of *Attenuatella*. He found that each brachidium in specimens of *A. incurvata* Waterhouse consisted of an anteriorly directed lamella which at the front of the shell gives rise to a semicircle-like structure parallel to the hinge of the shell (Waterhouse 1964, fig. 48). The brachidia of the

sectioned specimens of *A. convexa*, although initially similar to the preserved brachidia of *A. incurvata*, are more complete and they have enabled reconstruction of brachidia presumably characteristic of the genus (text-fig. 2) though those of the type species are unknown. Each brachidium of *A. convexa* consists of an anteriorly directed lamella

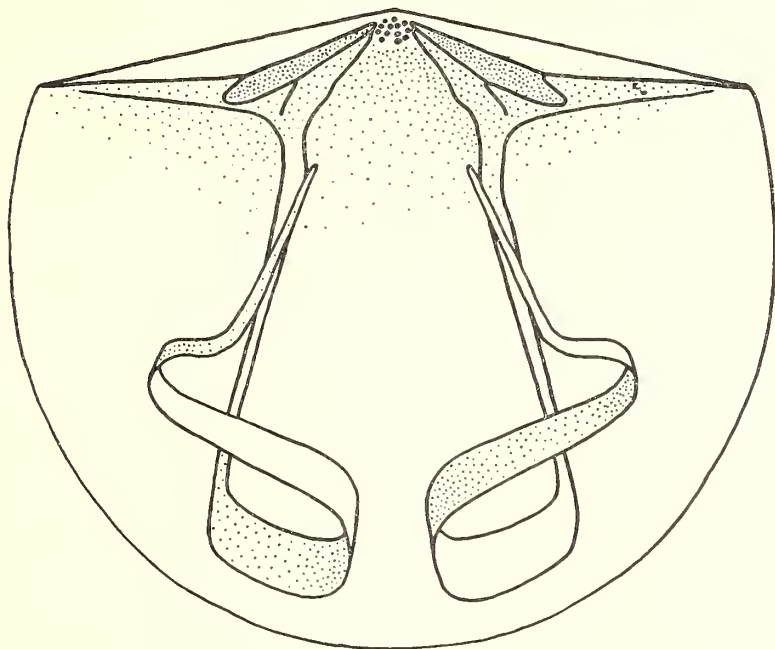


TEXT-FIG. 1. Serial acetate peels of four (A, B, C, D) specimens of *Attenuatella convexa* sp. nov. The interval between successive sections is 0.25 mm. except where indicated, and in the latter cases the dimensions given on the diagram are in millimetres.

which leads into an S-shaped structure (text-fig. 1) from the ventral end of which there is a ventrally placed posteriorly directed lamella. The consistency of the arrangement of these features in the sectioned specimens of *A. convexa* suggests that they represent the complete brachial skeleton of the species. Spiral lamellae are not present in *A. convexa* but rather the brachial skeleton is basically loop-like with curious anterior modifications.

The nature of the brachidia of *Attenuatella* does not necessitate its reclassification. Indeed except for the fact that the spiralia characteristic of several members of the Ambocoeliinae (George 1931, Veevers 1959, Vandercammen 1956) are absent from

Attenuatella, the characteristics of *Attenuatella* completely support its classification in this subfamily. *Attenuatella* has an impunctate shell, a shell form which is comparable with other ambocoelins, a spinose micro-ornament, areas on both valves, and a non-striated tuberculate cardinal process. The placement of *Attenuatella* in the Ambocoeliinae is therefore maintained. A spiriferid having abbreviated brachidia resembling those of *Attenuatella* is the Middle Ordovician genus *Protozyga*. *Protozyga* possesses a jugum but otherwise each of its brachidia has the same basic form of a single volution parallel to the median plane of the shell as the brachidia of *Attenuatella*.



TEXT-FIG. 2. Diagrammatic reconstruction of an antero-ventral view of the brachidia of *Attenuatella convexa* sp. nov., based on serial acetate peels of ten specimens, four of which are shown in text-fig. 1.

The reason for the brachidial deviation in *Attenuatella* from the normal type of spiriferid spiral is problematic and it is conjectural whether the lophophore of *Attenuatella* had the form of a spiral. The shape of the brachidia of *A. convexa* does not preclude the presence of a spiral-like lophophore, and if such an organ did exist it appears that in general only the first flexured whorl of the lophophore was provided with a calcareous support. If the lophophore was not spirolophous but rather was confined to the reduced brachidia it is possible that the S-shaped brachidial modifications were developed to compensate the loss of length of the lophophore. In this instance the feeding organ was probably zygo-lophous. The brachial skeleton of *Attenuatella* seems to be of a more primitive type than the spiralia of other ambocoelins. Perhaps it is relevant that species of *Attenuatella* are the youngest known representatives of the Ambocoeliinae and that reversion to this loop-like arrangement in *Attenuatella* occurred not long before the extinction of the subfamily in the Upper Permian.

Genus *ATTENUATELLA* Stehli 1954*Attenuatella* Stehli; Chernyak 1963*Attenuatella* Stehli; Waterhouse 1964

Type species (original designation). *Attenuatella texana* Stehli 1954, pl. 25, figs. 31–3 from the lower part of the Lower Permian Bone Spring Formation, Texas, text-fig. 3 (1).

Diagnosis. Small essentially plano-convex spiriferids; ventral valve elongate, smooth, or sulcate, with elongate relatively narrow umbo and more or less incurved beak; ventral area apsacline; dorsal valve convex, flat, or gently concave with low area; ornament of small spines often arranged in concentric lines, and fine discontinuous radial grooves; each groove runs anteriorly for a short distance from a spine; field of muscular attachment in ventral valve an elevated platform; no plates support the teeth; crural plates sessile and cardinal process tuberculate; shell impunctate.

Other species and specimens

A. acutirostris (Krotova) 1885, pl. 4, fig. 24 of Artinskian age from the Ural Mountains in Russia, text-fig. 3 (2).

A. stringocephaloides (Chernysheva and Likharev) in Likharev and Einor 1939, pl. 13, fig. 5a, b from Abrosimov Bay, Novaya Zemlya, text-fig. 3 (3). According to Likharev and Einor (1939, p. 189) a number of the species occurring with *A. stringocephaloides* at Abrosimov Bay (Likharev and Einor 1939, p. 185) also occur in the Spirifer Limestone and Brachiopod Chert in Spitzbergen. Likharev and Einor further intimate (p. 188) that all of the faunas of Novaya Zemlya are to be equated with the faunas of the Spirifer Limestone and the Brachiopod Chert for which Stepanov (1957) has suggested either an upper Lower Permian or a lower Upper Permian age or perhaps both (i.e. belonging to his Svalbardian Stage).

A. attenuata (Cloud) 1944, pl. 17, figs. 22–5 from the Wordian *Waagenoceras* Zone in Mexico, text-fig. 3 (4).

A. stringocephaloides (Chernysheva and Likharev); Chernyak 1963, pl. 42, figs. 3 and 4 from the lower Baykura sub-horizon of eastern Taimyr, text-fig. 3 (5). Ustritskiy and Chernyak (1963) correlate the lower Baykura sub-horizon with the lower Vorkuta Series in the Pechora Basin and they consider that both of these units correspond to the Ufa Suite on the Russian Platform. Stepanov (1957) intimated that the latter Suite should be included in the Svalbardian Stage which he proposed (1957) for faunas in Spitzbergen intermediate in aspect between the faunas of the Artinskian Stage and the Kazanian Stage. For this time interval Ustritskiy (1960) also proposed a new stage, the Paykhoyian Stage based on the fauna of the Vorkuta Series, and in 1963 Ustritskiy and Chernyak had little hesitation in referring the fauna of the lower Baykura sub-horizon to the upper part of Ustritskiy's stage. Ustritskiy and Chernyak also suggest, in view of the absence of a complete Permian section in Spitzbergen, that it might be preferable to recognize the Paykhoyian Stage rather than the Svalbardian Stage.

A. taimyrica Chernyak 1963, pl. 42, figs. 5–9 from the Byrranga horizon of eastern Taimyr, text-fig. 3 (6). Ustritskiy and Chernyak (1963) correlate the Byrranga horizon with a composite Artinskian–Kungurian Stage in the Ural Mountains.

A. incurvata Waterhouse 1964, pl. 20, figs. 1–12, pl. 21, figs. 1–9 from the Arthurton Group in New Zealand, text-fig. 3 (7). Waterhouse (1964, 1967) considers the fauna in this unit to be of Kazanian age.

A. sp. Landis and Waterhouse, 1966, pl. 1, figs. 1–5 from the Wesney Siltstone in the Eglinton Volcanics, New Zealand, text-fig. 3 (8). Landis and Waterhouse seem to be uncertain about the age of these specimens. They firstly state (p. 139) that the specimens 'are probably identical with Aktastinian (lower Artinskian) *Attenuatella* in the Takitimu Group', but later (p. 145) intimate a Kazanian age from their remark regarding the age of the Wesney Siltstone, that 'a Kazanian age is possible on an objective consideration of the fossils alone'.

A. sp. Landis and Waterhouse 1966, p. 144 also mention some specimens of *Attenuatella* from New Caledonia, and after a preliminary examination of the material they consider that the specimens could be conspecific with *A. incurvata*, text-fig. 3 (9).

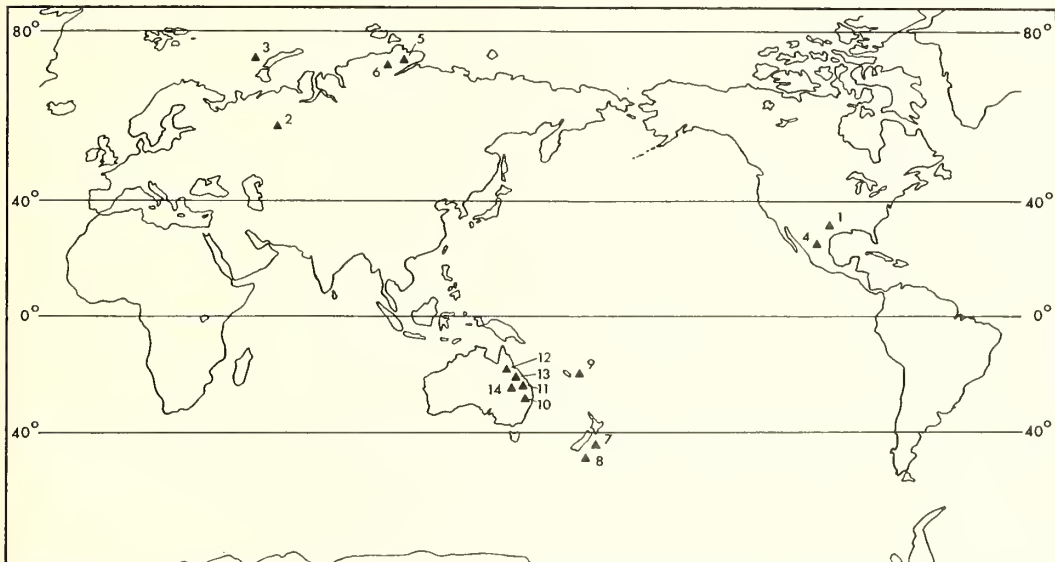
A. multispinosa Waterhouse 1967, pl. 24, figs. 1-7 from the Gilgurry Mudstone in the Boorook Group in northern New South Wales, text-fig. 3 (10). Waterhouse (1967, p. 172) considers that this species is likely to be of late Kungurian or early Kazanian age.

Australis Armstrong and Brown (1968) describe a new species from below the Gigoongan Limestone in the Maryborough Basin, Queensland, text-fig. 3 (11). They suggest a lower Artinskian (Aktastinian) age for the species.

A. convexa sp. nov. (see p. 788), text-fig. 3 (12).

A. sp. A (see p. 790), text-fig. 3 (13).

A. cf. incurvata (see p. 791), text-fig. 3 (14).



TEXT-FIG. 3. Global distribution of *Attenuatella*. Each solid triangle signifies at least one occurrence of the species nominated by the adjacent number. References to the numbers are in the text.

Comparison. *Attenuatella* is distinguished from *Crurithyris*, its closest relative by its narrower more elongate ventral valve and umbo, and the elevated platform of muscular attachment in the ventral valve. It is also possible to separate the genera on the nature of their brachidia. The brachial skeleton of *A. texana* is unknown. However, from the work of Waterhouse (1964) and from information gained from *A. convexa* it is known that each brachidium of these two species of *Attenuatella* consists essentially of an anteriorly directed lamella which eventually curves ventrally and then is deflected posteriorly to form a single volution parallel to the median plane of the shell. In contrast the brachial skeleton of *Crurithyris urii* (Fleming), the type species of *Crurithyris*, consists of laterally directed spires of from three to six whorls (George 1931, p. 40). Waterhouse (1964, p. 108) has further noted that on *I. incurvata* only one series of spines seems to be present whereas according to George (1931, pp. 51 and 55) there are two series of spines on *C. urii*. However, these differences may not be significant for on some specimens of *A. convexa* the spines are relatively uniform in size, and on others there are both large and small spines (Pl. 142, figs. 5, 12).

Another genus superficially similar to *Attenuatella* is *Moumina* Fredericks 1919

(1924), but unfortunately this genus has been little used or described since its institution. Moreover, the only description of *M. incertia* (Chernysheva), the type species of *Moumina* (OD; Fredericks 1919) is Chernysheva's original description of the general external appearance of the species.

Distribution. In addition to its occurrence in Australia, *Attenuatella* is found in New Caledonia, Russia, North America, and New Zealand. The global distribution is shown in text-fig. 3.

Range. Lower Artinskian (Aktastinian) to Kazanian or Wordian.

Attenuatella convexa sp. nov.

Plate 142, figs. 1–12, 19

Holotype. UQF53036 from UQL3127 in the lower part of the Tiverton Formation in the north-eastern part of the Bowen Basin, Queensland. (UQL3127, about half a mile east of Homevale Homestead, 20 miles north of Nebo on the Nebo–Collinsville road.)

Diagnosis. Ventral valve moderately inflated with a distinct sulcus, and a broad massive umbo that is not incurved over the area; commissure ligate; dorsal valve gently

EXPLANATION OF PLATE 142

All figures are $\times 4$ except where indicated

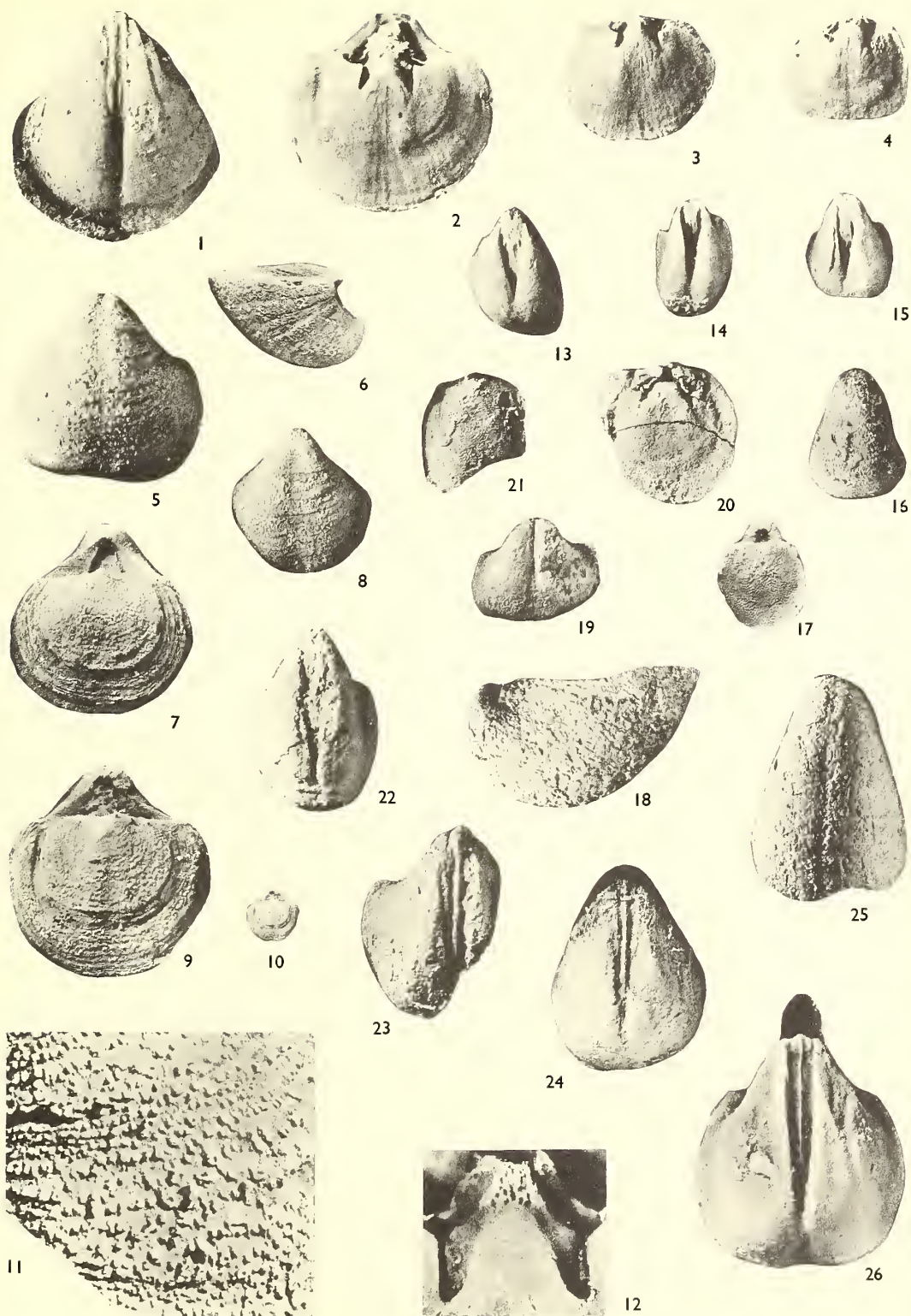
Figs. 1–12. *Attenuatella convexa* sp. nov. All specimens are from the Tiverton Formation at UQL3127, about half a mile east of Homevale Homestead, 20 miles north of Nebo on the Nebo–Collinsville road, Queensland. 1, Internal mould of ventral valve, UQF53029. 2, 3, 4, Internal moulds of dorsal valves (note impressions of areas of adductor muscle attachment in figs. 3 and 4), UQF53030, UQF53031, and UQF53032 respectively. 5, 8, Latex casts from external moulds of ventral valves (note two sizes of micro-ornamental spines on specimen in fig. 5), UQF53033 and UQF53034 respectively. 6, Lateral view of latex cast of external mould of both valves, UQF53035. 7, 9, Latex casts of external moulds of dorsal valve and umbo of ventral valve, UQF53036 (holotype) and UQF53037 respectively. 10, Same specimen as in fig. 9, Natural size. 11, Micro-ornament on a ventral valve $\times 17$ (note the relative uniformity in the size of the spines), UQF53038. 12, Internal mould of the umbonal part of a dorsal valve showing the impression of a tuberculate cardinal process $\times 12$, UQF53039.

Fig. 19. *Attenuatella* sp. cf. *convexa*. Postero-ventral view of internal mould of ventral valve. UQF47256, from the sandstone unit below the Upper Limestone near Gympie. The specimen is from the first ridge north of Rammut Road, three-quarters of a mile east of Chatsworth, 5 miles north of Gympie, south Queensland.

Figs. 13–18. *Attenuatella* sp. cf. *incurvata*. Waterhouse. 13, 14, 15, Internal moulds of ventral valves. CPC9018, CPC9019, and CPC9020 respectively from T111, 2.7 miles north-north-west of the Cracow–Theodore road crossing of Delusion Creek, 10 miles north-west of Cracow, Queensland. 16, Latex cast from an external mould of a ventral valve. CPC9021 from T111. 17, Latex cast from an external mould of a dorsal valve and the umbo of the ventral valve. CPC9022 from T111. 18, Lateral aspect of a ventral valve. CPC9023 from T111.

Figs. 20–3. *Attenuatella* sp. A. 20, Latex cast from external mould of dorsal valve. CPC9027 from T111. 21, Internal mould of dorsal valve. CPC9026 from Du151, 1 mile south-west of Bundaleer Homestead, 37.5 miles north of Bluff, Queensland. 22, 23, Internal moulds of ventral valves. CPC9024 and CPC9025 respectively from Du151.

Figs. 24–6. *Attenuatella* sp. 24, Internal mould of ventral valve. CPC9028 from Du764, 2 miles west-north-west of Bundaleer Homestead 37.5 miles north of Bluff, Queensland. 25, Latex cast of external mould of specimen in fig. 24. 26, Internal mould of ventral valve (note the absence of ridges along the margins of the platform of muscular attachment). GSQF3459 from GSQL D16, in the north-eastern corner of portion 359, Parish Walloon, Queensland.



to moderately convex having a wide median flattening bordered by low ridges for its entire length.

Description. The shell is biconvex with an elongate, moderately inflated ventral valve and a semicircular, gently to moderately convex dorsal valve. Cardinal extremities are obtusely rounded and the shell is usually widest at the mid-length of the dorsal valve. The ventral umbo is high, and relatively broad, but is not incurved over the area. The ventral area is apsacline and is about three times as high as the anacline dorsal area, both areas being separated from the remainder of their valves by distinct beak ridges. There is usually a narrow sulcus in the ventral valve corresponding to a median flattening or depression on the dorsal valve. Flanking the depression on the dorsal valve there are two low ridges. Otherwise the dorsal valve is gently convex, being slightly more so umbonally than towards the commissure. The commissure is ligate. The valves are externally ornamented with small variably sized spines which lie along vaguely concentric lines and are sometimes developed at the edges of growth lamellae. The lines of spines are between 0.1 and 0.3 mm. apart and along them 9 to 12 spines occur in each millimetre. On some specimens there are large spines interspersed with smaller ones (Pl. 142, fig. 5) whereas on other specimens the spines are relatively uniformly sized (Pl. 142, fig. 12). A small groove extends anteriorly for a short distance from each spine.

The internal features of the ventral valve of *A. convexa* are similar to those of *Attenuatella* sp. nov. of Armstrong and Brown (1968). There is little umbonal cavity thickening, and in the apical part of the delthyrial cavity there is a small delthyrial plate somewhat depressed below the level of the area. The musculature is similar to that of *Attenuatella* sp. nov. of Armstrong and Brown except that in *A. convexa* the ridges bordering the muscle platform are less prominent, especially posteriorly; the diductor scars are wider; and the platform of muscle attachment is generally less elevated posteriorly.

In the dorsal valve the sockets are prominent and they lie along the margins of the notothyrium. They are defined internally by prominent socket ridges, and medio-anteriorly confluent with each ridge and extending anteriorly for a short distance along the floor of the valve are the crural bases. From these arise anteriorly directed crural lamellae which give rise to the brachidia diagrammatically represented in text-fig. 2. The arrangement of the scars of adductor muscle attachment is shown in text-fig. 4. The cardinal process occupies the apical part of the delthyrium and is tuberculate, the tubercles being roughly arranged in rows radiating from the beak (Pl. 142, fig. 13).

Comparison. *A. convexa* is readily distinguished by its massive and only gently curved ventral umbo, its broad shell, and its convex dorsal valve. *A. taimyrica* from Russia is the species morphologically closest to *A. convexa*. According to Chernyak's description and figures, *A. taimyrica* shares with *A. convexa* a massive umbo, a gently concave ventral area and a narrow but distinct sulcus. *A. taimyrica* is, however, distinguished by its flat dorsal valve.

Distribution. A specimen from the sandstone unit underlying the Upper Limestone near Gympie is a representative of *Attenuatella convexa*. The specimen is an internal mould of a ventral valve which had a broad massive umbo and a relatively low muscle platform. This is the only known occurrence in addition to the type locality.

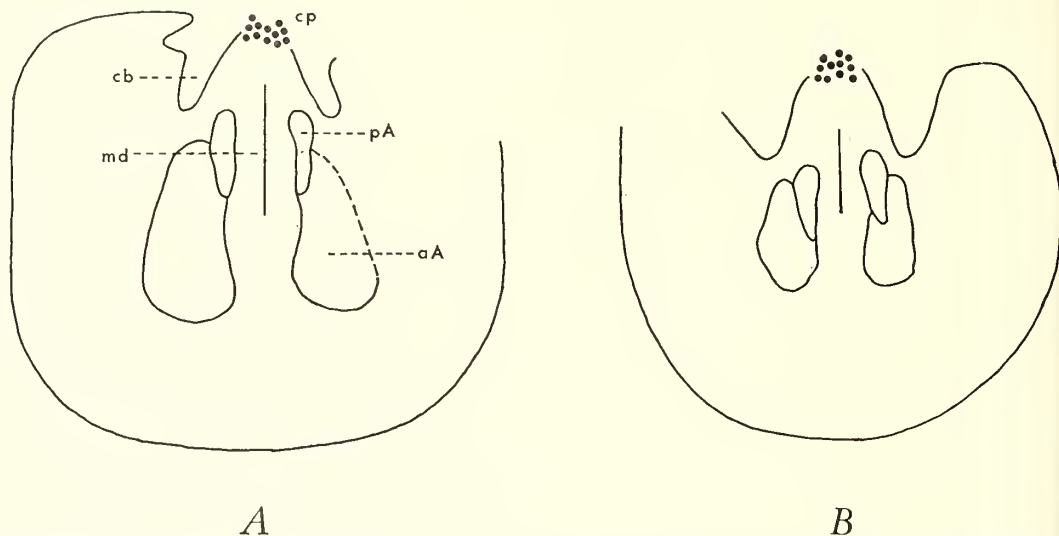
Age. The fauna occurring with *Attenuatella convexa* at the type locality is listed by Armstrong *et al* (1967, p. 89) in their record of the fauna which occurs with *Uraloceras lobulatum* Armstrong, Dear, and

Runnegar. Armstrong *et al.* suggest that the most likely age of this fauna is lower Artinskian (Aktasian) and the similarity between *A. convexa* and *A. taimyrica* provides a measure of support for this determination.

Attenuatella sp. A

Plate 142, figs. 20-3

Material. Several deformed internal moulds of ventral and dorsal valves (CPC9024-6) and a fragment of an external mould from Du151 (1 mile south-west of Bundaleer Homestead 37.5 miles north of Bluff, central Queensland).



TEXT-FIG. 4. Arrangement of the scars of muscular attachment in two dorsal valves of *Attenuatella convexa* sp. nov. A, UQF53031, and B, UQF53032 are figured respectively in Plate 142 figs. 3 and 4. cp, cardinal process; cb, crural base; md, median depression; pA, posterior abductor scar; aA, anterior abductor scar.

Description. Contour of ventral valve similar to that of *Attenuatella incurvata*; exterior of ventral valve unknown; dorsal valve gently convex and slightly elongate; it is less convex and narrower than dorsal valves of *A. convexa* but is more convex than dorsal valves of *A. incurvata*; on the fragment of external mould the spines number about 10 to 12 per mm. along roughly concentric lines; the interior of the ventral valve is similar to interiors of ventral valves of *A. incurvata* in that the ridges along the edges of the muscle platform are not as prominent as they are in *Attenuatella* sp. nov. of Armstrong and Brown, or in *A. multispinosa* Waterhouse.

Comparison. *Attenuatella* sp. A is distinguished from *A. incurvata* and *Attenuatella* sp. of Landis and Waterhouse by its elongate gently convex dorsal valve. *Attenuatella convexa* has a broader shell and a lower, more massive ventral umbo. The most closely comparable species are *A. stringocephaloides* and *A. attenuata* both of which have virtually non-sulcate ventral valves and flat or gently convex dorsal valves. The lack of internal details for *A. attenuata* and *A. stringocephaloides* of Chernysheva and Likharev and the lack of ventral exteriors of *Attenuatella* sp. A precludes complete comparison of these species. The interiors of the valves of Chernyak's specimens of *A. stringocephaloides* are known however and again in one of the ventral valves figured by Chernyak

there are only indistinct ridges along the edges of the muscle platform (Ustritskiy and Chernyak 1963, pl. 42, fig. 3a). Chernyak's specimens have flat dorsal valves and although they are thereby distinguishable from *Attenuatella* sp. A Chernyak's specimens seem to be morphologically closest to *Attenuatella* sp. A.

Distribution. A dorsal valve (CPC9027) from T111 (2.7 miles north-north-west of the Cracow-Theodore road crossing of Delusion Creek, 10 miles north-west of Cracow, Queensland) probably belongs to this species. It is elongate and gently convex, and diverging from the beak there are two low ridges separated by a broad median flattening. Spines on this valve number 12 per mm. along vaguely concentric lines.

Age. The specimens of *Attenuatella* which in one or another respect are morphologically close to *Attenuatella* sp. A are recorded from lower Upper Permian faunas suggesting possibly a similar age for *Attenuatella* sp. A.

Attenuatella sp. cf. *incurvata* Waterhouse 1964

Plate 142, figs. 13-18

Material. Several specimens (CPC9018-23) from the Barfield Formation at T111 (above).

Description. The specimens have elongate almost non-sulcate ventral valves with moderately inrolled beaks. The only dorsal exterior is very gently convex rostrally and slightly concave commissurally, and two ridges similar to those on the dorsal valves of *A. convexa* occur on its posterior part. Internal moulds of dorsal valves are more flat. There are about 12 spines per mm. on the valves. The interiors of the ventral valves are similar to those of specimens of *A. incurvata*. Only indistinct ridges occur along the sides of the areas of muscle attachment in the ventral valve, and there is a pronounced groove separating the adductor scars.

Discussion. The specimens from T111 are compared with *A. incurvata* on the basis of their non-sulcate ventral valves, on the shape and contour of their ventral and dorsal valves, and on the absence of prominent ridges along the edges of the platform of muscle attachment in the ventral valve.

Age. Lower Upper Permian?

Attenuatella sp.

Plate 142, figs. 24-6

Material. Two specimens (GSQF3459 and CPC9028). The first specimen is from the Flat Top Formation at GSQL D16 (in the north-eastern corner of portion 359, Parish Walloon, 3.3 miles north-east of Theodore, Queensland) and the other specimen is from Du764 (2 miles west-north-west of Bundaleer Homestead, 37.5 miles north of Bluff, central Queensland).

Description. Both specimens are internal moulds of ventral valves and are characterized by their posterior elongation and their incurved beaks. The external mould of the specimen from Du764 is non-sulcate. In the interiors of the valves there is an elevated platform of muscular attachment, but as in specimens of *Attenuatella* sp. A and *A. sp. cf. incurvata* only indistinct ridges occur along the sides of the platform. In both specimens the areas of adductor muscle attachment are separated by a prominent groove.

The specimens are probably conspecific with either *Attenuatella* sp. A or *A. sp. cf. incurvata* but the absence of dorsal valves in association with the specimens from D16 and Du764 does not permit their correct assignment.

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JOHN ARMSTRONG
Department of Geology
University of Queensland
St. Lucia
Brisbane, Queensland 4067
Australia

TAXONOMIC PROBLEMS IN THE STUDY OF COCCOLITHS

by MAURICE BLACK

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ABSTRACT. From a review of Jurassic, Cretaceous, Tertiary, and Recent coccolithophorid and discoaster material, it is suggested that the abrupt appearance of some complex forms, hitherto difficult to classify, may be explained by mineralization of already existing unmineralized stocks; it also seems likely that some living un-mineralized forms may have fossil mineralized ancestors. Some recent work on uncalcified Haptophyceae reveals interesting parallels with the coccolithophorids. One new family, Stephanolithiaceae, is erected, and four specific names are recorded in new combination.

LIVING in the present oceans there are about 200 species of coccolith-bearing algae. About half of these fall quite naturally into two big families; the rest make up a peculiarly heterogeneous collection, with numerous monospecific genera which are very difficult to group into families or higher taxa. Attempts to devise a scheme of classification for these organisms have not been entirely successful. The simpler schemes tend to force very diverse genera into an inappropriately small number of families, as may be seen in many reports on quantitative plankton-surveys. Some of the more elaborate schemes try to solve the problem by building up a theoretical phylogenetic tree which is used as a basis of classification. For this purpose, the evidence has been drawn exclusively from the comparative morphology of living species, and up to the present palaeontological observations have been almost completely ignored. Twenty years ago, this may have been excusable, but it is not so today, for there is now enough information at hand for us to start establishing phylogenetic series on the evidence of the fossil record.

When we attempt to do this, one of the first results is the discovery that the two largest families, the Syracosphaeraceae and Zygosphaeraceae, each with more than 50 living species, have virtually no geological record at all. With the smaller taxa, the situation is quite different; many of the systematically isolated genera are found to have long ancestries, and some are survivors from once prosperous Mesozoic or Tertiary families. Clearly, these survivors are more closely related to their own fossil ancestors than they are to living genera of different parentage, and it is no longer reasonable to lump all the living coccolith-bearing algae into a single family, as has been done in some of the most recently published classifications (Kamptner 1958, pp. 68-71, Deflandre 1966, pp. 5-6).

Considerations such as these suggest that the time has now arrived when we must look carefully at the impact of palaeontological research upon the taxonomy of living forms. During the last two decades there has been a strong tendency to deny the possibility of recognizing fossil representatives of many living taxa above the rank of species. This is, of course, a strictly logical attitude, because the micropalaeontologist has to work largely with individual coccoliths, and some modern genera are defined in terms that take into account the way in which the coccoliths are assembled to form a complete skeleton. Nevertheless, I think it is an unnecessarily defeatist attitude, because it assumes that each fossil coccolith is to be considered as a completely isolated entity, with no

ancestors and no descendents. This, of course, is not true, and I hope to show that many living taxa can be traced back with reasonable confidence into the Tertiary, and a few can be followed still further into the Mesozoic. In this way, family relationships sort themselves out as phylogenetic lineages, and the theoretical difficulties of working with isolated coccoliths fall into the background.

PROBLEMS IN THE CLASSIFICATION OF LIVING COCCOLITHOPHORES

From the early days, it has been found satisfactory to identify and classify the living species on the basis of coccolith-structure. No two species are known which have exactly similar coccoliths, and, as a working hypothesis, it is not unreasonable to assume that this also holds good for extinct species. Coccolith-structure has likewise been relied upon extensively for the delimitation of genera, but other characters such as the shape of the cell and the presence or absence of a naked area at the flagellar pole have also been used to some extent in defining genera and higher taxa. Living taxa defined purely in terms of coccolith-morphology can be recognized with certainty when they are found as fossils, but characters involving the arrangement of coccoliths on the cell-surface are not as a rule observable in fossil material. With this difficulty in mind, some micropalaeontologists have argued that all fossil coccoliths should be assigned to provisional taxa until a complete coccosphere has been discovered. This practice has the serious disadvantage of requiring a dual nomenclature, with one set of names for living material and another for fossils, thus creating an artificial break between modern forms and their fossil ancestors.

In order to resolve this problem, we will first of all look more closely at some of the taxonomic difficulties presented by living coccolithophores, and then try to discover just how serious these difficulties really are when we try to work out some sort of phylogenetic story.

Dimorphism of coccoliths

Lohmann (1902) found that in some species the coccoliths covering a single individual were not all alike; for example, those round the flagellar pole might bear spines, whereas the ordinary body-coccolith did not. Usually the polar coccoliths are easily recognizable as straightforward modifications of the normal type, and Lohmann did not in general segregate species with this kind of dimorphism into separate genera. The only genus which he distinguished on these grounds was *Scyphosphaera*, which has an equatorial girdle of very large float-coccoliths. Taxonomic difficulties did not arise until 40 or 50 years later, when Kamptner (1941) and Deflandre (1952) took a much more serious view of coccolith-dimorphism, and removed all species with dimorphic coccoliths into separate genera. The consequent practical difficulty in naming fossil coccoliths was perhaps unnecessarily exaggerated, but the theoretical implications led Deflandre to abandon the use of a single classification for both living and fossil forms, and to create an independent taxonomic system for the fossils. The general adoption of this policy during the decade that followed did much to retard progress in the study of phylogenetic and taxonomic relationships among the fossil coccoliths.

Coccolith-dimorphism is likely to have been prevalent to much the same extent in

fossil as in living taxa, and although final proof is usually beyond our reach, it is not difficult to find fossil examples of morphological variants that have all the earmarks of dimorphic pairs. These are not uncommon in *Cretarhabdus* (Pl. 150, figs. 4, 5), *Deflandrius* (Pl. 151, figs. 4, 5), *Kamptnerius* (Pl. 152, figs. 5, 6), and *Rhabdolithina*; if fossil species with dimorphic coccoliths are not recognized as such, the worst that can happen is that two species with identical ranges appear in the fossil record instead of one.

Pleomorphic life-histories

Observations on the life-histories of species kept in culture have brought to light several examples in which a motile coccolith-bearing phase alternates with a sessile uncalcified phase which had previously been accepted as a member of a different genus (Parke 1961). This is particularly true of coastal species, whose non-motile phases tend to live attached to rocks. Distinct from these are the pelagic species, whose resting-stages take the form of calcified cysts, which in the absence of any solid support, remain suspended in sea-water. One of these species, *Crystallolithus hyalinus*, which bears organic scales, sometimes unmineralized (Pl. 154, figs. 1, 2), and sometimes covered with minute rhombohedra of calcite, has proved to be the motile phase of *Coccolithus pelagicus*, an encysted form with coccoliths of a totally different kind (Pl. 143, figs. 1, 2).

These unexpectedly complicated life-histories are interesting from a taxonomic point of view, because the individual phases are usually so different from each other that they were put into separate genera when first discovered. To judge from our knowledge of living species, we can hardly expect to find tangible evidence of pleomorphism in the fossil record. In the coastal species, all the known sessile phases are uncalcified, and hence unlikely to be preserved as fossils. In the pelagic species, on the other hand, it is only the heavily calcified cysts, or their component coccoliths, that stand much chance of being preserved; delicate motile forms like *Crystallolithus* soon disintegrate, and are never found in bottom deposits. Indeed, material from living cultures needs careful handling in the laboratory to prevent the organic scales from losing their cover of calcite crystals. The cysts, on the other hand, are often preserved entire, and good examples are quite common in rocks as old as the Kimeridge Clay (Pl. 143, fig. 6).

Variation in response to external conditions

Changes in external conditions can, in some circumstances, cause the organism to modify the appearance of its coccoliths, or even to cease calcification.

In most species that have been experimented upon, the principal effect of temperature-change is to alter the rate of cell-multiplication, without any significant effect upon coccolith-morphology. In *Coccolithus huxleyi*, however, the coccoliths grown in warm water are reported to be distinguishable from those grown at low temperatures (Pl. 145, figs. 1, 2); the two variants have been recorded in laboratory cultures (Watabe and Wilbur 1966) and in natural populations (McIntyre and Bé 1967).

C. huxleyi is kept in culture in several laboratories, and a number of separate strains are kept under constant observation. Some of these have been found quite suddenly to stop growing coccoliths, and to persist in a naked condition (Paasche 1964, p. 11). One cause of this change appears to be an enrichment in the supply of nutrients, particularly phosphate. An interesting point is that whereas some strains will resume growth

of coccoliths if the culture medium is adjusted to a composition more like natural seawater, others will not, and no known treatment will induce them to do so.

There are several very suggestive possibilities here in connection with the evolution and taxonomy of these algae; fixation of a single phase out of a pleomorphic life-history, independent development of ecological variants, and sudden changes from a naked to a calcified condition, could all lead to the introduction of apparently cryptogenetic forms into the geological record. Furthermore, some of these changes could take place very suddenly, owing to the extraordinarily fast rate of multiplication that is prevalent in these organisms (Parke and Manton 1962).

PHYLOGENETIC HISTORY OF SOME LIVING TAXA

Attempts to trace living coccolithophorids back into geological history lead to curiously divergent results. Some species such as *Coccolithus pelagicus*, *C. huxleyi*, and *Braarudosphaera bigelowi* lead back to flourishing and diverse complexes, which in the present oceans have been reduced to just one or two surviving representatives. The ancestral stocks show a good deal of evolutionary divergence, but a set of unifying family characters persists throughout. *Pontosphaera* provides an extreme example of divergence, for we not only get a hint of an evolutionary connection with the extinct Zygolithaceae, but we also find here the first suggestion of a far-distant linkage with another living family, the Helicosphaeraceae. Other stocks seem to have been peculiarly stable throughout their geological history. *Calciosolenia* can be traced back to mid-Cretaceous times with very little change, and the coccoliths of *Braarudosphaera bigelowi* are specifically indistinguishable from fossils preserved in early Cretaceous rocks. In contrast with these are two flourishing modern families, the Syracosphaeraceae which are abundantly represented in contemporary Globigerina Ooze, but have not been found in deposits older than Quaternary, and the Zygospaeraceae which are not represented in bottom deposits at all.

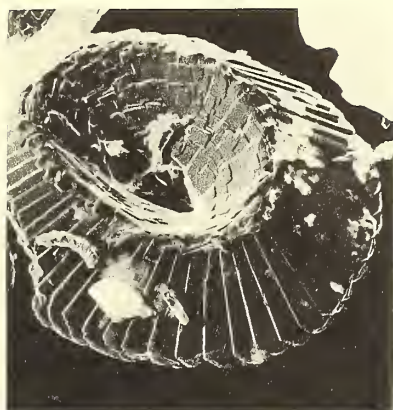
Coccolithus pelagicus (Wallich) Schiller

Plate 143, figs. 1, 2

This is the most familiar of all coccoliths; it was discovered in samples of ooze raised from the floor of the North Atlantic Ocean during the first telegraph surveys, and was examined by Huxley and Wallich, and later by Murray and Blackman (1898). The living

EXPLANATION OF PLATE 143

- Figs. 1, 2. *Coccolithus pelagicus* (Wallich) Schiller, recent Globigerina Ooze, *Discovery II* Sta. 4269, Biscay Abyssal Plain. 1, No. 20175, oblique distal view, $\times 4800$. 2, No. 5000, details of central area, distal view, $\times 5000$.
- Fig. 3. *Coccolithus* sp. cf. *C. cavus* Hay and Mohler; No. 22279, Upper Oligocene, core DWBG 10, Pacific Ocean; distal view, $\times 5300$.
- Fig. 4. *Coccolithus* sp. cf. *C. marismontium* Black; No. 22284, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view, $\times 6700$.
- Figs. 5, 6. *Ellipsagelosphaera* sp. 5, No. 15230, Campanian Chalk, Belgorod, Russia; distal view, $\times 8000$. 6, No. 22874, Cambridge Greensand, Cherry Hinton Fields, near Cambridge; complete coccosphere (calcified cyst), $\times 3700$.



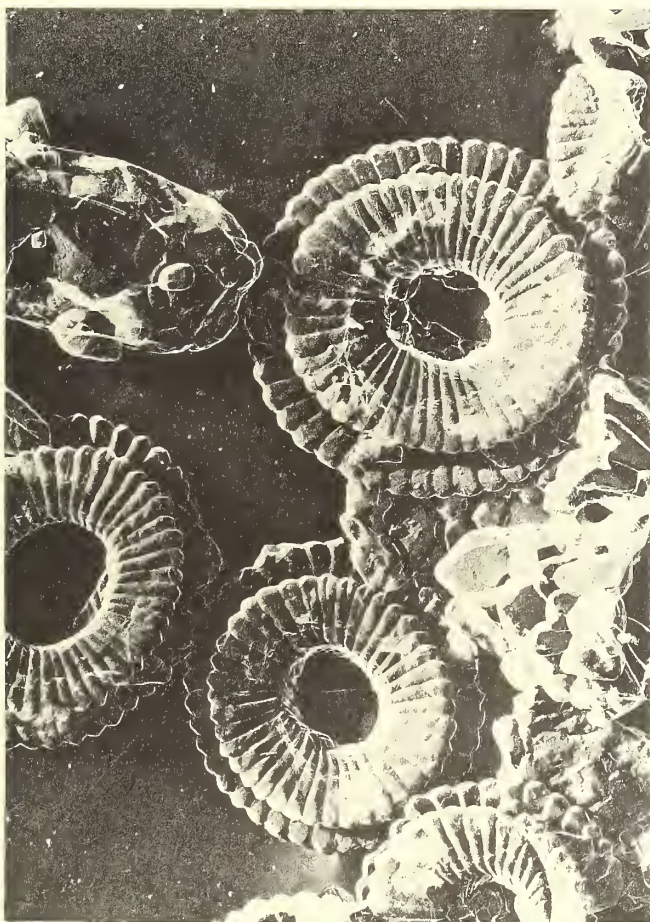
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alga is confined to the North Atlantic, and is the only species that is known to have a preference for cold water; all attempts to find it in Antarctic waters of suitable temperature have failed. This was apparently not the case during the Pleistocene, for Allan Bé and his colleagues at the Lamont Observatory have found it in core-samples from the southern oceans at levels dated as belonging to the middle of the Wisconsin glacial episode (McIntyre and Bé 1967). In the Tertiary, there are very similar forms, but studies under the electron microscope show that they are specifically distinct (Pl. 143, fig. 3). The same generic form can be traced back to the Eocene, but once we pass into the Mesozoic, the species that superficially resemble *C. pelagicus* are obviously different in the finer details of their construction. When the coccoliths are examined under a petrological microscope, with the fossil lying flat on the slide, Tertiary and living species give an interference figure in which the distal shield plays no part, since the optic axes of the component calcite crystals are at right-angles to the plane of the shield. In the Mesozoic genus *Ellipsagelosphaera* this is not the case, and the crystals of the distal shield show strong birefringence, so that the optical figure takes a complicated form, due to the superposition of two black crosses, one produced by each shield. In addition, the Mesozoic species always have a corona of quadrate or keystone-shaped crystals lying on top of the distal shield, and marking off the central area (Pl. 143, fig. 5). Under an ordinary microscope the Tertiary and Mesozoic species look very much alike, but under a polarizing microscope or an electron microscope they are so obviously distinct that they are now placed in separate subfamilies.

In the Jurassic and Cretaceous there are also several other genera such as *Sollasites* (Pl. 144, figs. 1, 2), which resemble *Coccolithus* in a general way, but differ considerably in the finer details of their structure. They are clearly not on the main line of descent towards the *C. pelagicus* stock, but some of them may prove to be ancestral to certain other Tertiary and living forms.

Cyclcoccolithus leptoporus (Murray and Blackman) Kamptner

Plate 144, figs. 3, 4; Plate 147, fig. 1

On theoretical grounds, Kamptner has argued that the circular outline is more primitive than the elliptical, and has insisted upon the taxonomic separation of these two shapes (compare Pl. 143, figs. 1–6, Pl. 144, figs. 3–7). He remarks:

‘Above all else, one clear-cut taxonomic principle is decisive for subdivision . . . into tribes and subtribes: a sharper separation of the circular from the elliptical forms. A primitive character must be attributed to the circular outline, and a derivative character to the elliptical. . . . It is also *a priori* conceivable that the change-over from the circular to elliptical types has been achieved polyphyletically, and so to speak on a broad front’ (Kamptner 1958, p. 64).

In accordance with this principle, he removed *Coccolithus leptoporus* to a new genus, *Cyclcoccolithus*, and similarly split up other genera so that species with circular coccoliths could be put into different subtribes from those with elliptical coccoliths.

Cyclcoccolithus leptoporus provides a convenient starting point from which to examine this taxonomic principle in relation to the geological record. This species is abundant in the living plankton, and is widely distributed. Very similar coccoliths are common in the Pliocene, and particularly so in core-samples from the ocean floor (Pl. 144, fig. 4).

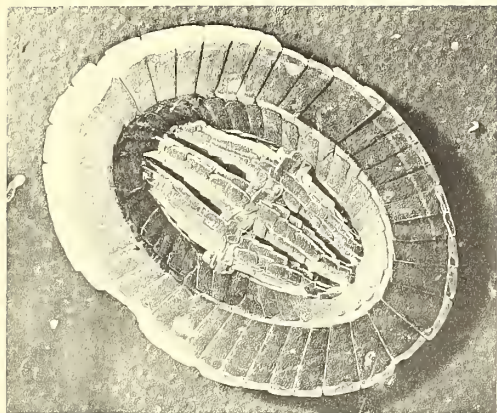
In such deposits, the two discs of the placolith are apt to become separated, and many records of *Tiarolithus* and *Calcidiscus* from the Upper Tertiary are probably based upon dismembered specimens of *C. leptoporus* or closely related species. Other species are found in the Lower Tertiary, and the earliest record of the genus is from the Danian. These early forms occur associated with characteristically elliptical species of *Coccolithus*, and the two stocks were quite distinct from each other at the time of their first appearance in the early Tertiary. Thus the Tertiary record does not give much support to the idea that the circular shape is primitive; indeed, it tends to emphasize the complete independence of the elliptical forms rather than to provide any suggestion of their descent from circular ancestors.

This independent relationship is emphasized by a curiously similar state of affairs in the Upper Jurassic, for a different set of circular and elliptical types exist side by side in the Oxford and Kimeridge Clays. These include the genera *Cyclagelosphaera* and *Ellipsagelosphaera* (Noël 1965), which at first sight appear to be so much like *C. leptoporus* and *C. pelagicus* that they were originally recorded under these names. This resemblance, however, is illusory, for there are significant differences in micro-structure. It is remarkable that the two Jurassic genera each differ from their Tertiary analogues in exactly the same way: they both have strongly birefringent distal shields, surmounted by a well-developed corona (compare Pl. 143, fig. 3 and Pl. 144, fig. 3 with Pl. 143, fig. 5 and Pl. 144, fig. 5). Consequently, if we focus our attention on the minutiae of crystal-arrangement, we find that the Jurassic circular forms resemble their elliptical contemporaries more closely than they resemble modern circular forms. Are we then to unite the Jurassic genera, both circular and elliptical, into one family or subfamily, as Noël (1965) has done, or would it be more reasonable to keep the two shapes separate, regarding them as two parallel stocks that became independent at an early stage, and have remained so ever since?

An attempt to answer this question requires a closer look at the geological history of these two stocks. The elliptical forms are abundant throughout the Mesozoic and Cainozoic, and it may be that within this multitude of species there exists a continuous evolutionary thread leading from the Jurassic to the present day. The only serious break in this record is at the Cretaceous–Paleocene boundary, and there is not enough information available at present to reach a decision. The history of the circular placoliths is rather different. After the great abundance of *Cyclagelosphaera* (Pl. 144, fig. 5) in the Jurassic, there is a paucity of circular forms in the Cretaceous. The few examples that

EXPLANATION OF PLATE 144

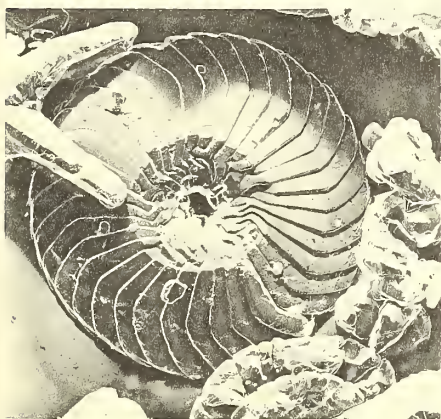
- Figs. 1, 2. *Sollasites horticus* (Stradner *et al.*) comb. nov. (= *Coccolithus horticus* Stradner *et al.*), Cambridge Greensand near Cambridge, $\times 9600$. 1, No. 4706, Barrington, distal view. 2, No. 21739, Cherry Hinton Fields, proximal view.
- Figs. 3, 4. *Cyclcoccolithus* spp., Lower Pliocene, core LSDH 78P, Pacific Ocean. 3, cf. *C. leptoporus* (Murray and Blackman) Kamptner, No. 22224, distal view, $\times 4000$. 4, No. 22210, group with some specimens in the 'Calcidiscus' condition, $\times 2500$.
- Fig. 5. *Cyclagelosphaera margereli* Noël; No. 17410, Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole; distal view, $\times 10\,000$.
- Fig. 6. *Markalius* sp. cf. *M. inversus* (Deflandre) Bramlette and Martini; No. 17199, Belemnite Marl (L. Turonian), Cherry Hinton, near Cambridge; proximal view, $\times 6000$.
- Fig. 7. *Ericsonia* sp.; No. 22295, Upper Oligocene, core DWBG 10, Pacific Ocean; proximal view, $\times 6000$.



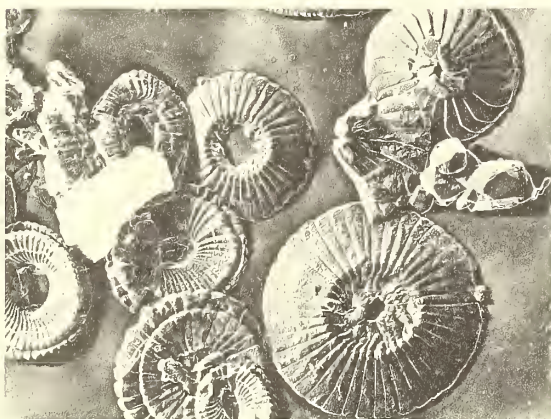
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are known, such as *Markalius* (Pl. 144, fig. 6), can hardly be regarded as linking *Cyclagelosphaera* with *Cyclococcolithus*, because they have a more complicated structure than either of these. They seem rather to be leading towards *Ericsonia* (Pl. 144, fig. 7) and other still more specialized forms that flourished in the Lower Tertiary. There is thus a gap extending throughout the Cretaceous period, during which they were apparently no representatives of the hypothetical *Cyclococcolithus* lineage. It seems, therefore, unlikely that the Tertiary species originated as an offshoot from *Cyclagelosphaera*, and it is more probable that they developed from an unknown ancestor early in the Tertiary.

The evidence from the geological record thus seems to alienate the Mesozoic circular forms from their modern analogues, and the evidence of morphology throws them into association with their elliptical contemporaries, in spite of the difference of shape.

Coccolithus huxleyi (Lohmann) Kamptner
(= *Emiliania huxleyi* (Lohm.) Hay and Mohler 1967)

Plate 145, figs. 1, 2

The taxonomic position of this species is surrounded by interesting problems. It stands apart from *C. pelagicus* and all other living members of the genus in the peculiar construction of its shields, and its conspicuous central grid, which recalls the similar structures in many extinct forms. Mary Parke in Parke and Dixon (1964, p. 520) has pointed out that the motile phase lacks an obvious haptonema, and in this respect it resembles the Isochrysidales rather than the Coccolithophorales. Paasche (1964, p. 11) found in his cultures that coccolith-secreting individuals were without visible flagella, although these could be seen on some of the naked cells.

In the living plankton, it is undoubtedly the most vigorous and successful of the coccolith-bearing algae. It is distributed over the whole area of the oceans from the Antarctic convergence to the Arctic, and can invade brackish waters inaccessible to other pelagic species. Because of its great vigour and tolerance, it has provided material for more laboratory experiments than any other species.

C. huxleyi is apparently a very recent addition to the oceanic plankton. McIntyre and Bé (1967) have reported its first appearance in deep-sea cores as taking place within Brunhes Normal Zone (that is, less than 700 000 years ago, and more probably nearer to 100 000 years). They also report the presence of a coccolith intermediate between *C. huxleyi* and *Gephyrocapsa oceanica* in cores spanning the interval between 300 000 and 100 000 years. *G. oceanica* (Pl. 145, fig. 3) can be traced back into the Pliocene, and survives in the living plankton. Forms with the oblique bridge characteristic of *Gephyrocapsa* are unknown before the Pliocene, but the other characters of the genus, such as the large central opening with a bilateral grid, and the non-imbricate ray-elements, are strongly developed in a host of Lower Tertiary species of *Tremalithus* (Pl. 145, figs. 4–6). There is a great diversity of species with elaborate grids in the Middle and Upper Eocene, and the same type of coccolith can be traced back still further into the Mesozoic. The earliest representatives, with rather simpler grids, are found in the Lower Gault (Middle Albian) at Folkestone (Pl. 145, figs. 7, 8).

The taxonomic isolation of *C. huxleyi* from the rest of the genus *Coccolithus*, which is suspected from the peculiarities of the living alga, is thus confirmed by its long and independent geological history, and there can be little doubt that this species should be

removed to a separate genus, and possibly to a family independent of the Coccolithophoraceae.¹

Pontosphaera discopora Schiller

Plate 146, figs. 1, 2

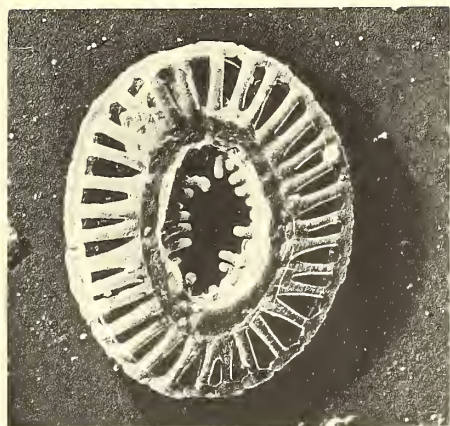
The genus *Pontosphaera* was created by Lohmann (1902) for species in which the coccoliths appear to be simple discs, with or without a shallow rim. The outline is elliptical, and the coccoliths are most commonly shaped like a shallow pie-dish. Specific diagnoses were originally based upon work under the biological microscope, and later studies in polarized light or under the electron microscope have led to the removal of several species to other genera. No electron micrographs of the type species, *P. syracusana*, have yet been published, but Mrs. Gaarder has generously allowed me to compare some of her excellent micrographs of this species with my Tertiary material. The coccoliths are large, with a floor perforated by about 750 very delicate pores, and the wall is constructed of about 200 very slender and steeply inclined calcite laths. *P. discopora* has similarly constructed but smaller coccoliths, with larger and less numerous pores. The Tertiary coccoliths discussed below have the same general type of structure, and can with reasonable confidence be referred to the same genus as *P. syracusana* and *P. discopora*.

Coccoliths of various species of *Pontosphaera* are not uncommon in modern Globigerina Ooze, particularly beneath the warmer parts of the oceans. In the Pliocene a form closely resembling *P. discopora* is occasionally found (Pl. 146, figs. 4, 5), but other species are rare or absent, and none of the modern perforated species has yet been identified with certainty in pre-Pliocene sediments. Nevertheless, coccoliths with all the characteristic features of *Pontosphaera* except the circular pores in the floor, are widely distributed throughout the Tertiary. There appear to be several lineages among these Tertiary species, each with a slightly different pattern in the structure of the floor. One of these is of special interest, since it appears to connect the living *P. discopora* with a complex of Eocene forms whose ancestry can probably be traced back to the Cretaceous. The proximal surface of the floor in this series has a bilateral arrangement of plates similar to that originally described by Kamptner in *P. scutellum*, and now known in a number of diverse Eocene forms (Pl. 146, fig. 6). The distal side has an entirely different

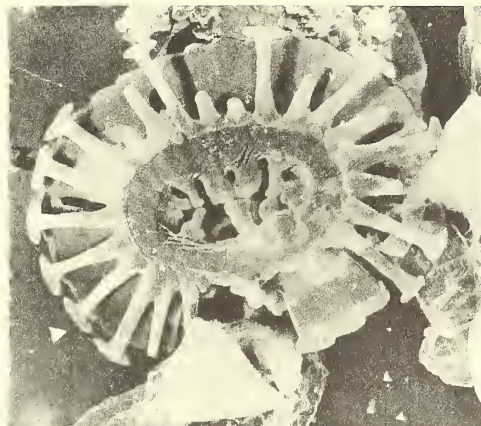
EXPLANATION OF PLATE 145

- Figs. 1, 2. *Coccolithus huxleyi* (Lohmann) Kamptner; recent oceanic deposits. 1, warm-water form, No. 3421, *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 16\ 000$. 2, cold-water form, No. 11612, *Discovery II* Sta. 3809, Galicia Bank; distal view, $\times 20\ 000$.
 Fig. 3. *Gephyrocapsa oceanica* Kamptner; No. 18072, modern Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts., proximal view, $\times 8000$.
 Figs. 4-8. *Tremalithus* spp. 4, *T. danicus* (Black) comb. nov. (= *Dictyococcites danicus* Black); No. 11819, Middle Oligocene, Grundf r, Denmark; proximal view, $\times 6000$. 5, *T. placomorphus* Kamptner; No. 22838, Lower Oligocene, Rodstenseje nr. Odder, Denmark; proximal view, $\times 4000$. 6, *T. dictyodus* (Deflandre and Fert) comb. nov. (= *Discolithus dictyodus* D. and F.); No. 22831, Lower Oligocene, Rodstenseje nr. Odder, Denmark (possibly reworked from M. Eocene); proximal view, $\times 6100$. 7, *T. burwellensis* Black; No. 14622, Cambridge Greensand (Cenomanian), Barrington near Cambridge; distal view with proximal shield showing through, $\times 10\ 000$. 8, *T. sp.*, No. 13371, Lower Gault (M. Albien), Folkestone, Kent; proximal view, $\times 8000$.

¹ Since this lecture was delivered, a paper by W. W. Hay *et al* has been received, in which *C. huxleyi* has been formally transferred to a new genus, *Emiliania*.



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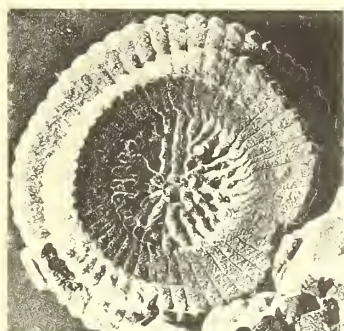
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appearance, with a pattern of concentrically arranged fibrous elements (Pl. 146, figs. 3, 7). This combination of patterns is also seen in several species of *Helicosphaera* (Pl. 147, figs. 1-3), and will be considered further in connection with the ancestry of that genus.

This constructional pattern can be picked up again in the late Cretaceous. Two species in the Santonian and Campanian have the same kind of wall-structure, and the same arrangement of plates on the proximal surface. One of these, *Pontolithina moorevillensis*, has two small perforations at the foci of the ellipse (Pl. 149, fig. 4). This species may well prove to be the ancestor of several Tertiary lineages. Obliteration of the two pores and an increase in the number of wall-elements would give a form very much like certain Eocene species, for example *P. versa* Bramlette and Sullivan (Pl. 146, fig. 6), *P. vadosa* Hay *et al.*, and possibly other forms like *Discolithus oamaruensis* Defl. Enlargement of the pores to make two circular windows would lead to such forms as *D. duocavus* Bram. and Sull. (L. Eocene) and *D. panarium* Defl. (M. Eocene).

There are also several Eocene species which differ in having numerous small circular pores, but which probably have a comparable floor-structure, since they give similar interference patterns in polarized light; their ultra-structure has not yet been examined under the electron microscope. *D. punctosus* Bram. and Sull. (L. Eocene) and *D. distinctus* Bram. and Sull. (M. Eocene) have this structure; they foreshadow the modern perforate species of *Pontosphaera*, but in the absence of any recognizable intermediates in the Upper Eocene and Miocene, we cannot say whether there is any direct phylogenetic connection. Possibly *D. vigintiforatus*, the type species of *Discolithus* from the Miocene of the Vienna basin, may yet prove to be on this line of descent.

There can be little doubt that *Pontosphaera* has a long geological history, and that many Tertiary species that have been referred to the rather unsatisfactory form-genus *Discolithus* actually fit quite naturally into one or other of the lineages of this complex. A derivation from some branch of the Mesozoic Zygothaceae seems quite possible, and is indeed suggested by the presence in the Upper Cretaceous of forms that are intermediate between the two families (Pl. 149, fig. 4).

Helicosphaera carteri (Wallich) Kamptner
(= *Helicopontosphaera kamptneri* Hay and Mohler 1967)

Plate 147, figs. 1, 2

In the present-day oceans, the genus *Helicosphaera* is represented by a single species whose coccoliths are peculiar in having a spiral brim which terminates in a characteristically flaring wing. Within this brim is an elliptical shield, shaped rather like the crown of a hat; it has bilaterally arranged plates on the proximal side, and concentric fibres on the distal, so that the structure is much the same as in many species of *Pontosphaera*.

This species has been customarily regarded as closely related to, and possibly derived from taxa such as *Coccolithus* with typical placoliths. Study of *H. carteri* under the electron microscope does not give much support to this idea; the coccoliths are clearly not mis-shapen placoliths, as is often assumed, and it is difficult to see how the spiral flange could have been derived from the two shields of a placolith. Compared with other living coccolithophorids, *H. carteri* stands very much by itself, and its geological history abundantly confirms its independence from the Coccolithophoraceae.

At the present day *H. carteri* is confined to the parts of the oceans lying roughly between latitudes 50° N. and S.; in bottom sediments its range is withdrawn a little towards the equator (McIntyre and Bé 1967, p. 585). In the Pliocene, forms that would be difficult to separate from this species are widely distributed, both in deep-sea cores and in samples collected on land. Similar forms, still very much like *H. carteri*, are abundant in the Upper Miocene, but here they are associated with several extinct species which are obviously quite different. In the underlying parts of the Miocene and in the Oligocene and Eocene there is a varied complex of extinct species, and the genus was evidently undergoing a burst of evolutionary diversification, possibly at its climax during the Oligocene.

In the early Eocene there are several species whose coccoliths lack the broad, flaring wing that is so characteristic of later species; they have a shape that does not depart much from an ovoid or even a regular ellipse. The earliest of these, *H. seminuulum*, evolves from a Lower Eocene population in which this simple type (subspecies *seminuulum*) is predominant (Pl. 147, fig. 4), to a Middle Eocene population in which the predominant subspecies *lophotus* is much more like a typical *Helicosphaera* (Bramlette and Sullivan 1961). The rim in subsp. *seminuulum* shows little more than a suggestion of spiral structure, and in fact resembles the wall of an early Tertiary *Pontosphaera* crossed by an oblique wrinkle. The resemblance between these primitive species of *Helicosphaera* and some of the contemporary species of *Pontosphaera* is so close that they might reasonably be placed in the same genus, were it not that forms like *H. seminuulum* are so plainly ancestral to other more typical species of *Helicosphaera*.

We have thus traced the ancestry of *H. carteri* back to an early stage when the genus was barely distinguishable from *Pontosphaera*, and we are now in a better position to assess its taxonomic status. It clearly has no close relationship with the Coccolithophoraceae, and must be placed in some other family. It has sprung from the same ancestors as the living *Pontosphaera*, and for this reason might be included in the Pontosphaeraceae. On the other hand, it can be argued that the divergence between the two stocks since the early Tertiary has been so profound that the living representatives can hardly be included in a single family, and I have proposed elsewhere that a new family, the *Helicosphaeraceae*, should be established for *H. carteri* and the numerous Tertiary species of which it is the sole survivor (Black 1968).

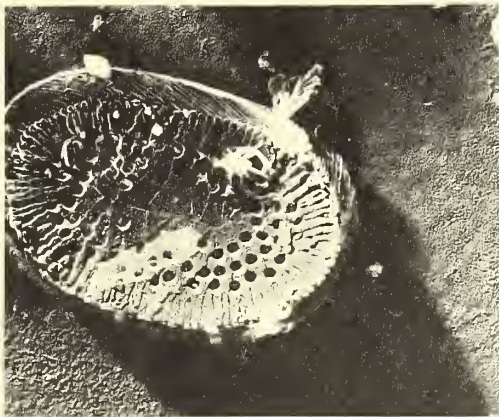
Braarudosphaera bigelowi (Gran and Braarud) Deflandre

Plate 147, fig. 5

In 1935 a new species, thought to be a *Pontosphaera*, was recorded in plankton hauls from the Bay of Fundy (Gran and Braarud 1935); this was re-examined by Deflandre,

EXPLANATION OF PLATE 146

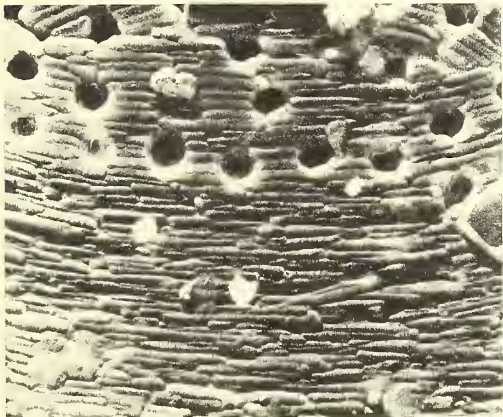
Figs. 1-7. *Pontosphaera* spp. 1-3, *P. sp. cf. P. discopora* Schiller, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean. 1, No. 11393, proximal view, $\times 7200$. 2, No. 11318, distal view, $\times 8000$. 3, No. 11319, details of distal surface, $\times 24\ 000$. 4, 5, *P. sp. cf. P. discopora* Schiller, Pliocene, Cisano nr. Albenga, Italy. 4, No. 16852, proximal view, $\times 4800$. 5, No. 16854, oblique proximal view, $\times 4000$. 6, 7, *P. versa* (Bramlette and Sullivan) comb. nov. (= *Discolithus versus* B. and S.), Eocene, Tuilerie de Donzacq, Landes, France. 6, No. 15855, proximal view, $\times 6000$. 7, No. 15834, distal view, $\times 6000$.



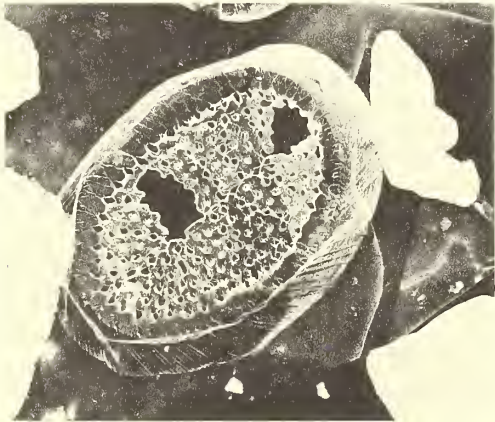
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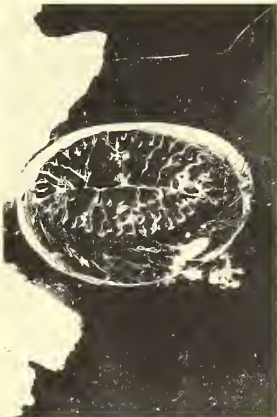
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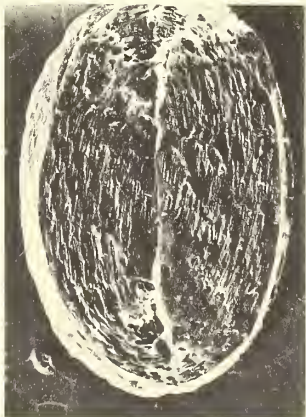
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who showed that its coccoliths were entirely different from any previously known form. They consist of five peculiarly shaped calcite plates arranged to form a regular pentagon, and twelve of these pentoliths fit together to make a dodecahedral skeleton enclosing an encysted cell. The species was re-named *Braarudosphaera bigelowi*, and a new family was based upon it (Deflandre 1947). At that time little was known about its geological history, which we now know to be quite remarkable. Coccoliths with exactly the same structure have been found at various levels in the Tertiary, and are abundant in the Upper Bracklesham Beds of the Sussex coast. They have also been found, though less abundantly, throughout the Cretaceous system, and except for an increase in size in the older specimens, are specifically indistinguishable from recent material. No other species of coccolithophorid has a stratigraphical range at all comparable with this, and at first sight it might be thought that we have here an extreme example of specific stability. This is no doubt true of the main lineage of *B. bigelowi* itself, but in the Tertiary we are confronted not only with a multiplicity of other species of *Braarudosphaera* itself, but in addition an exuberant development of two closely related genera, *Micrantholithus* and *Pemuna* (Pl. 147, fig. 6), all with coccoliths constructed on the same pentolith system. Detailed phylogenies have still to be worked out, but some of the simpler forms are so close to *B. bigelowi* that there can be little doubt about their origin.

B. bigelowi is an unquestionable example of a single living species that is the sole survivor of an important and diversified Tertiary family whose ancestry can be traced back well into the Mesozoic. This point is stressed because there are several other species in the living plankton with very much the same kind of history, resulting in a taxonomic isolation which is equally real, but by no means always so obvious.

CALCIOSOLENIACEAE Kamptner

Plate 148, figs. 1, 2

Most coccolithophorids have a spherical, egg-shaped, or pear-shaped body. The Calciosoleniaceae differ in being cylindrical or fusiform, and their coccoliths instead of being circular or elliptical, take the form of a narrow parallelogram (Pl. 148, fig. 1). There are probably four or five living species, and although the family characters are unmistakable, their systematics at generic and specific levels are not easy. Fossil representatives are never common, but have been found at intervals in the geological column down to the Cretaceous, the earliest British occurrence being at the base of the Cenomanian (Pl. 148, fig. 2); Stradner (in Stradner *et al* 1968) has recently announced the discovery of similar specimens in the Albian of Holland. The interesting feature of this record is that the earliest specimens differ so little from living material: the family characters with all their eccentricities are fully developed at the first appearance, there is no clue at all about relationships to other coccolith taxa, and no suggestion of any evolutionary change during the long interval from the middle Cretaceous to the present day.

LIVING FAMILIES WITH NO KNOWN GEOLOGICAL RECORD

We have now considered a number of isolated species in the living plankton, many of which have turned out to be survivors of once flourishing families that are otherwise

extinct. In contrast with these are the two largest living families, the Syracosphaeraceae and Zygosphaeraceae, which have no fossil record behind them. Both families have more than 50 species, and together they account for more than half the living coccolithophorids. The Zygosphaeraceae are all holococcoliths: that is, they are constructed of minute rhombohedra or prisms of calcite, each enclosed in an organic membrane. Such structures are very delicate, and would probably break down into their component crystals soon after falling to the sea floor; this may well be the reason why they are not found in the Globigerina Ooze or other oceanic deposits. This, however, can hardly be true of the Syracosphaeraceae, which are much more robustly constructed. Many species of *Syracosphaera* are, indeed, found abundantly in the modern Globigerina Ooze, and their absence from the Pliocene and older deposits therefore calls for some different explanation. (W. W. Hay and his colleagues have recently referred two Tertiary species to this genus (*S. bisecta* Hay *et al.* 1966, p. 393, and *S. clathrata*, 1967, p. 449). *S. bisecta* has been re-examined by Bramlette and Wilcoxon (1967, p. 102), who regard it as a species of *Coccolithus*, and until more is known about the wall-structure of *S. clathrata*, its reference to *Syracosphaera* cannot be regarded as fully established.) The obvious conclusion that the Syracosphaeraceae are, in fact, post-Tertiary additions to the oceanic plankton is probably correct, and will be considered later in relation to the abrupt appearance of other cryptogenic families in earlier times.

EXPLANATION OF PLATE 147

Figs. 1-4. *Helicosphaera* spp. 1, 2, *H. carteri* (Wallich) Kamptner, recent Globigerina Ooze. 1, No. 18030, *Discovery II* Sta. 4288, Biscay Mts., proximal view, $\times 7200$. Also *Cyclococcolithus leptoporus* (M. and B.) Kamptner, distal view. 2, No. 13137 from *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 7200$. 3, *H.* sp., No. 22839, Lower Oligocene, Rodstenseje nr. Odder, Denmark; proximal view, $\times 3200$. 4, *H. seminulum* Bramlette and Sullivan; No. 14293, Middle Eocene, core DWBG 23B, Pacific Ocean; proximal view, $\times 6700$.

Figs. 5, 7. *Braarndosphaera* spp. 5, *B. bigelowi* (Gran and Braarud) Deflandre; No. 15730, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; complete coccolith of five plates, $\times 4000$. 7, *B. africana* Stradner; No. 16057, Sutterby Marl (Aptian), borehole Alford, Lincs., 101-7 ft.; complete coccolith, $\times 4000$.

Fig. 6. *Penma papillatum* Martini; No. 15871, Yazoo Formation (Upper Eocene), Clarke County, Mississippi; single plate, $\times 5000$.

EXPLANATION OF PLATE 148

Fig. 1. *Calciosolenia* sp., No. 13131, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; proximal view, $\times 10\ 000$.

Fig. 2. *Scapholithus* sp., No. 20678, Chalk Marl, (Cenomanian), Folkestone, Kent; proximal view, $\times 13\ 000$.

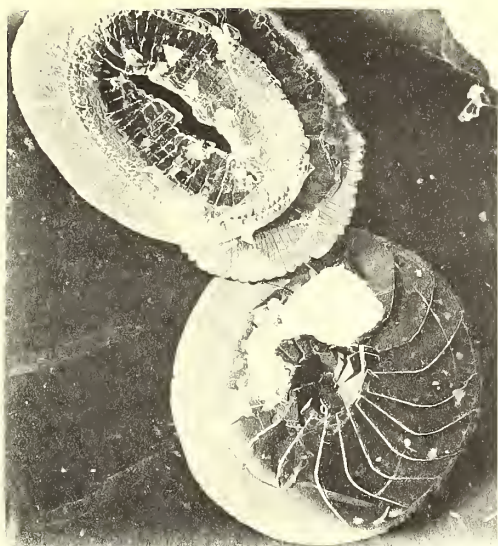
Figs. 3, 4. *Syracosphaera* spp. 3, *S. hystrica* Kamptner; No. 2573, recent Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean; distal view, $\times 16\ 000$. 4, *S. pulchra* Lohmann; No. 18062, recent Globigerina Ooze, *Discovery II* Sta. 4288, Biscay Mts.; proximal view, $\times 6000$.

Fig. 5. *Loxolithus armilla* (Black) Noël, holotype, No. 2807, Burwell Rock (Cenomanian), Great Shelford nr. Cambridge; distal view, $\times 8000$.

Figs. 6, 9. *Rhabdolithina* spp. 6, *R.* sp., No. 18616, Sutterby Marl (Aptian), borehole, Alford, Lincs., 101-7 ft.; oblique proximal view, $\times 6000$. 9, *R.* sp., No. 13501, Lower Gault (Albian), Folkestone, Kent; oblique proximal view, $\times 8000$.

Fig. 7. *Stanrolithites* sp., No. 21747, Cambridge Greensand (Cenomanian), Cherry Hinton Fields nr. Cambridge; distal view, $\times 8000$.

Fig. 8. *Zygodolothus diplogrammus* Deflandre; No. 22337, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; distal view, $\times 5300$.



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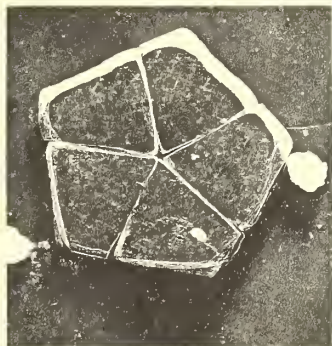
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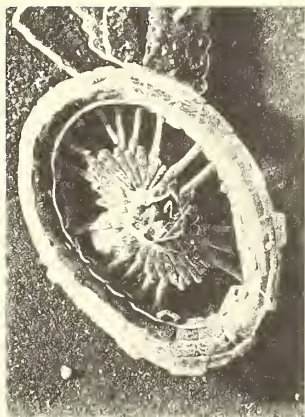
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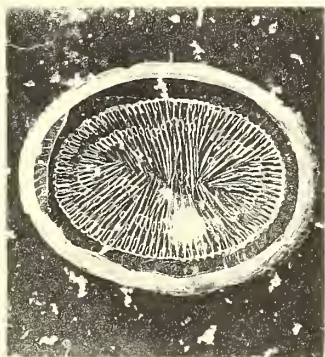
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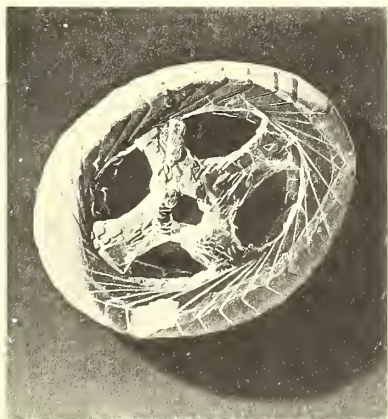
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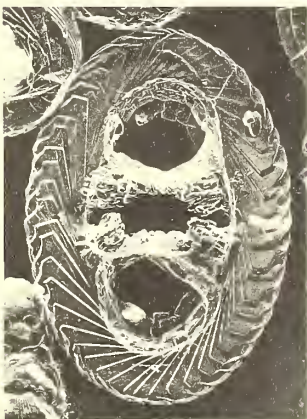
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EXTINCT FAMILIES

In examining the fossil representatives of living families, we have not found it necessary to employ a dual classification with the extinct species segregated into parataxa. We can approach the extinct families in much the same way, and follow the well-tried palaeobotanical practice of treating them as being made up of closely related organ-genera. Much depends upon the choice of characters that are relied upon for the definition of genera or families, and there must always be an element of personal opinion in making this selection. Quite clearly, we cannot follow any hard and fast rules, for some kinds of criteria that are of great value in certain families are worthless in others. For example, in the Zygolithaceae and Podorhabdaceae, the number of crystals in the marginal shields or rings is variable, even within a single species; in the Deflandriaceae, however, the number is always 16 (Pl. 151, fig. 2), and in the Braarudosphaeraceae it is 5 throughout the whole family (Pl. 147, fig. 5). In a large number of families the structure of the outer margin of the coccolith follows a characteristic pattern, and can be used as a primary basis of classification. Thus, the Zygolithaceae all have an architecture based upon the loxolith-ring (see below and Pl. 148, fig. 5); the Coccolithophoraceae have two marginal shields of radial elements (Pl. 143, fig. 4; Pl. 144, fig. 2; Pl. 145, fig. 3), and the Podorhabdaceae have yet another type of rim (Pl. 150, figs. 1, 6). The presence or absence of a central spine is also of unequal significance in different families. Such structures are characteristically present in the Rhabdosphaeraceae, but never in the Coccolithophoraceae. In the Podorhabdaceae, on the other hand, the coccoliths of some genera, such as *Polypodorhabdus* (Pl. 150, fig. 1) always have spines, but in others, such as *Cretarhabdus*, some coccoliths in a single species may have spines and others not (Pl. 150, figs. 4, 5). This state of affairs is also known in some living genera, such as *Syracosphaera*.

ZYGOLITHACEAE Noël

Plate 148, figs. 5-9; Plate 149, figs. 1-5

A large number of Mesozoic coccoliths have an outer wall that consists of narrow, steeply inclined laths of calcite, giving a structure rather like the wall of a barrel that has been given a sharp twist, so that the staves run obliquely instead of straight up and down (Pl. 148, figs. 6, 9). The resulting loxolith-ring resembles the wall of *Pontosphaera* in its general plan of construction, but differs in normally having no floor, and in having a much smaller number of staves, which are also coarser and more robust. The numerous genera which make up the family are defined by the various structures that bridge or partly close the opening within the ring.

The name *Loxolithus* was proposed by Denise Noël (1965) for species consisting of an unmodified ring (Pl. 148, fig. 5); many fossils preserved in this condition are in fact damaged specimens of other genera, having lost the bridge or central cross that was originally present. In *Zygolithus* there is a bridge along the shorter axis of the ellipse on the proximal side (Pl. 148, fig. 8). *Pontolithus* has a grid on the proximal side and a distal bridge (Pl. 149, figs. 2, 3), and *Staurolithites* has a central cross (Pl. 148, fig. 7). In several genera the proximal side of the loxolith-ring is closed by a floor, sometimes solid, but frequently pierced by pores (Pl. 149, fig. 1). In *Rhagodiscus* the floor consists

of a mosaic of little granules, and the addition of a prominent spine gives a rhabdolith-like appearance to *Rhabdolithina* (Pl. 148, figs. 6, 9).

The earliest Zygolithaceae are found in the Lias, but there is no great variety of structure until the Lower Cretaceous, when specialized forms begin to appear, leading up to the spectacular diversity of genera and species in the Albian and Cenomanian. High in the Upper Cretaceous there are species with a new type of floor-structure, in which the plates are arranged very much as in early species of *Pontosphaera* and *Helicosphaera* (compare Pl. 149, fig. 4 with Pl. 146, fig. 6 and Pl. 147, fig. 3). These have been mentioned already in connection with the ancestry of these two genera.

PODORHABDACEAE Noël

Plate 150, figs. 1-6

This is an exclusively Mesozoic family which made its first appearance in the Oxfordian, when five well-differentiated genera appeared simultaneously without any known ancestors. Most of these continue throughout the upper part of the Jurassic and the Lower Cretaceous. An additional genus, *Cretarhabdus*, appears in the Berriasian and continues with undiminished vigour to the top of the Maestrichtian, when this genus, and with it the whole family quite suddenly became extinct (Bramlette and Martini 1964). The characters of the family may be seen in Plate 150, figs. 1-6; there is an elliptical shield with a narrow rim consisting of two layers of keystone-shaped crystals surrounding a very large central area, from which arises a tall spine. The several genera which make up the family are distinguished from each other by the structures occupying the central area (compare Pl. 150, figs. 1, 2, 3, 5); in most of them the central spine is supported by four buttresses constructed of fibrous crystals. This is an architectural feature which is not confined to the Podorhabdaceae (Pl. 149, fig. 6; Pl. 151, fig. 3; Pl. 152, fig. 1), and its taxonomic significance will be discussed on a later page.

EXPLANATION OF PLATE 149

Fig. 1. *Zygolithus* sp. with perforated floor; No. 22407, Cambridge Greensand (Cenomanian), Hauxton Mill near Cambridge; proximal view, $\times 8000$.

Figs. 2, 3. *Pontolithus flabellus* (Stradner), comb. nov. (= *Coccolithus flabellus* Stradner), Cambridge Greensand (Cenomanian). 2, No. 22881, Cherry Hinton Fields, proximal view, $\times 6000$. 3, No. 11510, Barrington, distal view, $\times 8000$.

Figs. 4, 5. *Pontolithina* spp. 4, *P. moorevillensis* Black, No. 22362, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; proximal view, $\times 4800$. 5, *P.* sp., No. 22899, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; distal view, $\times 4800$.

Fig. 6. *Eiffellithus turiseiffeli* (Deflandre) Reinhardt, No. 22114, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; distal view with characteristically oblique spine, $\times 4000$.

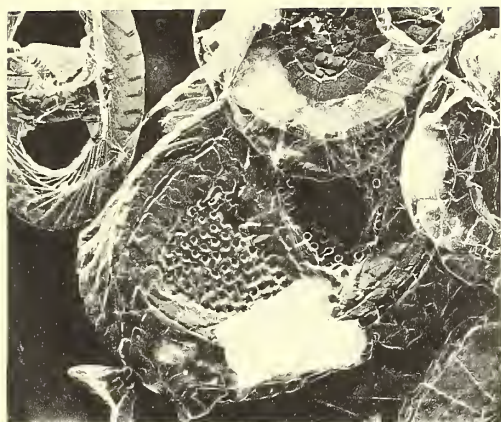
EXPLANATION OF PLATE 150

Fig. 1. *Podorhabdus cylindratus* Noël, No. 22798, Upper Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole, 220 ft. 3 in.-221 ft. 3 in.; distal view, $\times 4800$.

Fig. 2. *Polypodorhabdus madingleyensis* Black, No. 17413, Oxford Clay, locality as 1; distal view, $\times 9600$.

Fig. 3. *Ethmorhabdus gallicus* Noël, No. 22799, Oxford Clay, locality as 1; distal view, $\times 7200$.

Figs. 4-6. *Cretarhabdus* spp., Cambridge Greensand (Cenomanian) nr. Cambridge. 4, No. 21766 with spine, Hauxton Mill; distal view, $\times 4800$. 5, No. 21763 without spine, Cherry Hinton Fields; distal view, $\times 9600$. 6, No. 22867, Cherry Hinton Fields, side view, $\times 4800$.



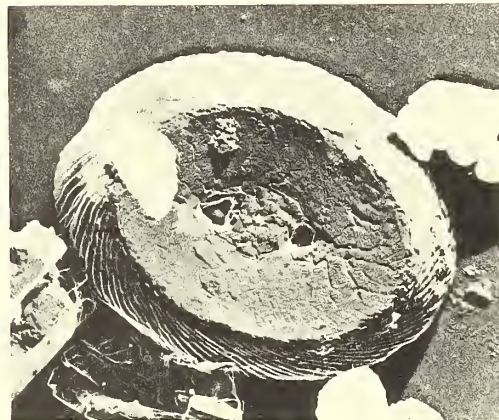
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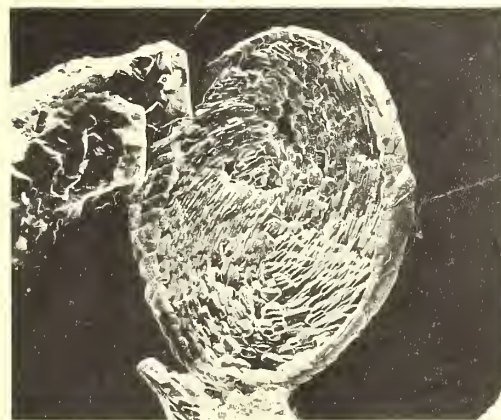
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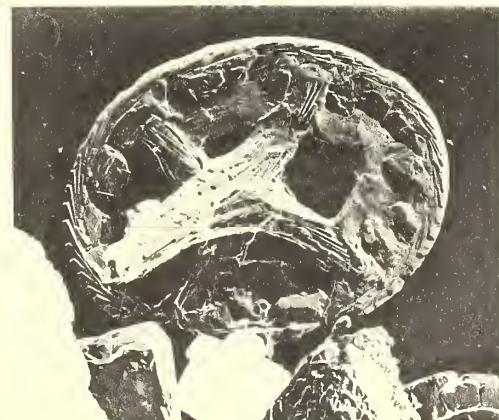
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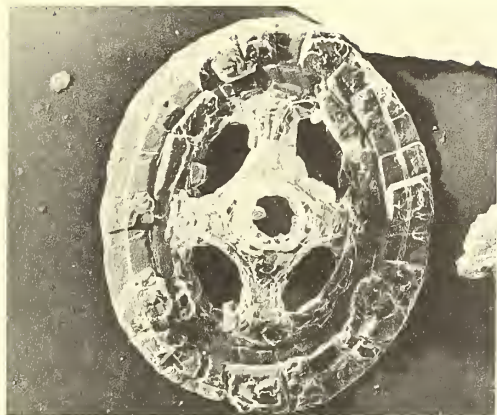
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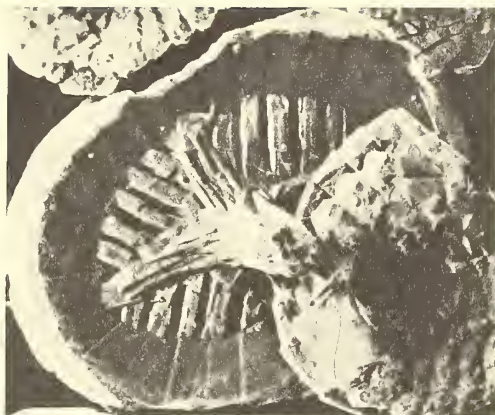
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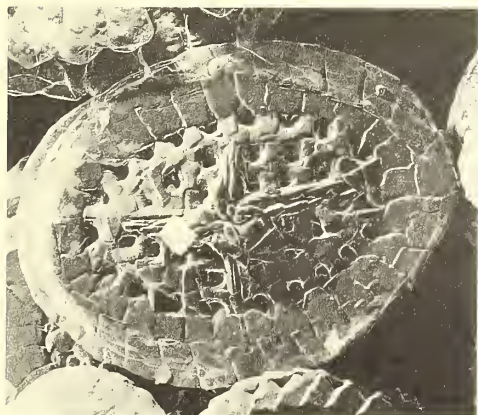
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DEFLANDRIACEAE Black 1967

Plate 151, figs. 1-5

More than a century ago Sorby described a remarkable coccolith from the Chalk; it has a ring of sixteen granules from which arise four flying buttresses supporting a peculiarly constructed stalk. Bramlette and Martini (1964) have shown that Sorby's coccolith belongs to one of several closely similar species that existed in the Upper Cretaceous, and which they united into the genus *Deflandrius*. The earliest species is found in the Gault (Pl. 151, fig. 1); it has all the family characters fully developed, and has no known ancestors. Three distinct, but very similar species are very abundant in the Upper Cretaceous right up to the top of the Maestrichtian, when the whole family became extinct.

The main differences between this family and the Podorhabdaceae are to be found in details of ultra-structure. Otherwise the two families share the same basic architectural plan: a spine supported by four buttresses arising from a granular ring. Quite recently, this structural plan has been found to be developed in a remarkably similar way among the uncalcified Haptophyceae, notably in several species of *Chrysochromulina*. This discovery raises the possibility that the ancestors of both the *Deflandriaceae* and *Podorhabdaceae* may have belonged to such uncalcified stocks in which the family characters were already developed, and only needed the ability to calcify in order to make their appearance on the geological record.

GONIOLITHACEAE Deflandre

Plate 151, fig. 6

This is perhaps the most remarkable of the extinct families. It was founded by Deflandre (1957) upon a single species, *G. fluckigeri*, which he discovered in the Eocene of north-west Germany and the Oligocene of Basses Alpes. The coccolith is pentagonal in outline, with a granular centre and radially constructed border. More recently, Martini (1964) has discovered a complete cyst in the Clayton Formation (Danian) of Alabama; in this unique specimen, twelve of the pentagonal coccoliths are fitted together to form a regular dodecahedron, giving a configuration exactly like the cysts of *Braarudosphaera*, but with an entirely different coccolith-structure. Martini has shown that *G. fluckigeri* ranges from the Lower Maestrichtian to the Rupelian, in the later occurrences apparently re-worked. The only observable difference between earliest and latest autochthonous specimens is a slight increase in size. Although *Goniolithus* is always a rare fossil, it has a wide geographical distribution: Denmark, France, Germany, English Channel (submarine core-samples), Tunisia, Alabama, and Texas. At the time of writing, the family still includes only the single species.

STEPHANOLITHIACEAE fam. nov.

Plate 152, figs. 1-3

The genus *Stephanolithion* was created by Deflandre (1939) for a peculiar species of coccolith from the Oxford Clay of Calvados, which he named *S. bigoti*. It differs from other coccoliths in having a set of radial spines extending beyond the marginal ring;

moreover, each spine consists of a single scalenohedron, a crystal habit that is most unusual among the coccolithophorids. Two more species have subsequently been discovered: *S. speciosum*, also from the Oxford Clay, and *S. laffitei* from the Portlandian of Algeria. *S. bigoti* is known from the Callovian, but is only common in the Oxfordian; in England it appears to be confined to the Upper Oxford Clay. *C. laffitei* is now known to occur throughout the Cretaceous System, becoming extinct at the top of the Maestrichtian.

Stephanolithion stands so far apart from other coccoliths that it cannot be fitted into any existing family, and I propose a new family name, Stephanolithiaceae, with the characters of the single included genus.

DISCOASTERACEAE Tan Sin Hok

Plate 153, figs. 1-9

The discoasters are usually considered to be taxonomically distinct from the coccoliths, but it would be unrealistic to ignore the likelihood that they are the products of similar planktonic algae, possibly in an encysted condition. They are mentioned here because they illustrate particularly clearly the taxonomic importance of crystal-orientation, which these organisms were able to control with great precision. In most species of *Discoaster* no crystal outlines are visible; nevertheless, the orientation of the crystals can be determined optically, and they are invariably found to be arranged so that the c-axis lies parallel with the axis of symmetry of the discoaster. In a smear-slide prepared so that the fossils lie flat against the cover-slip, they consequently remain dark in all positions between crossed nicols, and show the maximum refractive index for calcite. This property is constant for all discoasters, and at once distinguishes them from typical coccoliths.

The general appearance of the discoasters can be seen in Plate 153, figs. 1-8. They

EXPLANATION OF PLATE 151

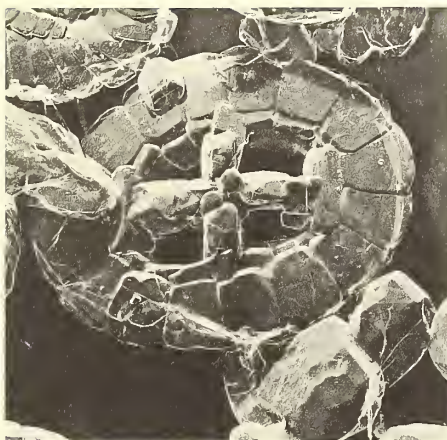
- Figs. 1-5. *Deflandrius* spp. 1, *D. cantabrigensis* Black, No. 22863, Cambridge Greensand (Cenomanian), Cherry Hinton Fields nr. Cambridge; side view, $\times 6000$. 2, 3, *D. spinosus* Bramlette and Martini. 2, No. 22187, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; oblique distal view, $\times 4000$. 3, No. 20144, Upper Chalk (Campanian), borehole at Holton nr. Halesworth, Suffolk; distal view, $\times 8000$. 4, 5, *D. cretaceus* (Arkhangelski) Bramlette and Martini. 4, No. 18481, Upper Chalk (Santonian), nr. Salisbury, Wilts.; oblique proximal view of short-stalked form, $\times 6000$. 5, No. 22321, Mooreville Chalk (Santonian), nr. Eutaw, Alabama; oblique proximal view, $\times 6000$. Fig. 6. *Goniolithus fluckigeri* Deflandre, No. 22888, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; damaged coccolith, $\times 10\,000$.

EXPLANATION OF PLATE 152

- Figs. 1-3. *Stephanolithion* spp. 1, *S. bigoti* Deflandre, No. 22783, Upper Oxford Clay (L. Oxfordian), Cambridge Experimental Borehole; distal view, $\times 4000$. 2, 3, *S. laffitei* Noël, Lower Gault (M. Albian), Folkestone, Kent. 2, No. 13503, proximal view, $\times 10\,000$. 3, No. 13537, oblique distal view, $\times 8000$. Fig. 4. *Neococcolithes* sp., No. 22923, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama; proximal view, $\times 10\,000$. Figs. 5-7. *Kamptnerius magnificus* Deflandre, Prairie Bluff Formation (Maestrichtian), Wilcox County, Alabama, $\times 4000$. 5, No. 22902, form with narrow wing, distal view. 6, No. 22928, form with expanded wing, distal view. 7, No. 22925, form with narrow wing, proximal view.



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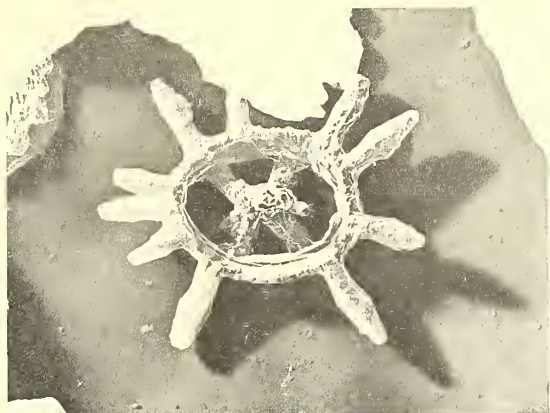
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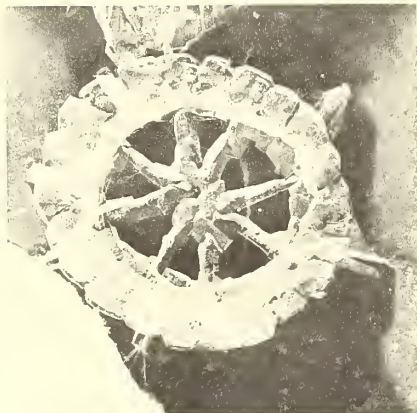
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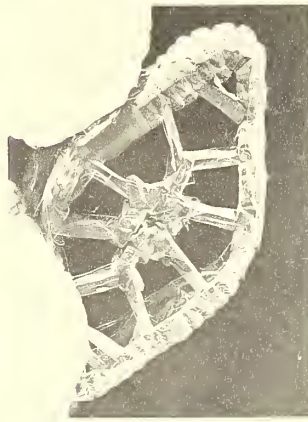
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consist of calcite crystals grouped round a central axis, giving a snow-flake pattern. In *Marthasterites* (Pl. 153, fig. 9) the whole structure appears to consist of a single calcite crystal. In *Discoaster* each ray is crystallographically distinct, as may be seen from the etch-patterns which are all too common on corroded specimens, or from the crystal faces that are sometimes seen in exceptionally well-preserved specimens (Pl. 153, fig. 1).

Marthasterites is found in the Upper Cretaceous and in the Lower Eocene; *Discoaster* is confined to the Tertiary, appearing in the Paleocene and becoming extinct at the top of the Pliocene or just within the Pleistocene, according to the horizon adopted for the base of the Quaternary. Reported discoveries of living *Discoasteraceae* are at present unconfirmed.

Constancy of crystal-arrangement is equally prevalent among the coccoliths; its optical effects, however, are much more complicated when the crystal-axes are not all parallel, but they are none the less of great taxonomic significance, and are relied upon extensively in systematic work. In the *Braarudosphaeraceae* the crystals are arranged round a central axis, much as in the *Discoasteraceae*, but the orientation is quite different, with the rhombohedron faces lying approximately in the plane of the coccolith (Pl. 147, fig. 5). In *Stephanolithion* the radial spines are scalenohedra with the optic axes at right angles to the central axis of the coccolith (Pl. 152, fig. 1). In the majority of coccoliths, the arrangement is much more complicated, with the optic axes arranged in a pattern that almost invariably involves some kind of screw symmetry.

RELATIONS WITH UNCALCIFIED STOCKS

The geological histories of the various coccolithophorid stocks discussed above clearly do not all follow the same pattern. On the one hand there are long-ranging stocks such as the *Coccolithophoraceae*, *Pontosphaeraceae*, and *Zygolithaceae*, with a great number of species spread out through a considerable span of geological time. These pass through phases when generic and specific distinctions are blurred, and evolutionary divergence was evidently taking place. The *Coccolithophoraceae*, for example, passed through such phases in Albian-Cenomanian times, again in the Eocene, and apparently once more in the Pleistocene. The taxonomic problems involved in this state of affairs are those familiar in any actively evolving group of organisms, and call for no special comment here.

In contrast with such normally evolving stocks, there are others which behave quite differently; these arrive on the scene abruptly, with all their characters ready-made. Some of them, for example *Goniolithus*, *Deflandrius*, and *Stephanolithion*, persist perhaps for the length of a geological period with little or no change, and then just as abruptly become extinct; others, such as the *Podorhabdaceae*, appear equally abruptly, but undergo noticeable evolutionary changes before they become extinct. In each of these cryptogenic stocks, there is a well-defined architectural plan which we have taken as characteristic of the family, and which is fully perfected in the earliest known species. It looks very much as though the architectural plan had already been elaborated before the fossil record started, and I think we have to consider seriously the possibility that the beginning of the fossil record for such a family simply marks the change-over to calcification in a stock whose scales were previously unmineralized.

Of course, we can hardly hope to find any tangible evidence of a palaeontological

nature to support this speculation, but fortunately there are other lines of investigation open to us. The most promising of these is an inquiry into the existing unmineralized stocks themselves, with a view to finding out what linkages may exist between these and the coccolith-bearing algae.

Recent work on the uncalcified Haptophyceae has indeed brought to light some very interesting parallels with the coccolithophorids. The various species of *Chrysochromulina* have been found to bear delicate organic scales, which in their architectural construction are very similar to some coccoliths. It is a little surprising to find that the most elaborately constructed scales, although quite unlike the majority of living forms, can be readily matched among extinct taxa.

In spite of their extreme tenuity, these scales apparently consist of two layers which are differently sculptured, and if calcified would produce entirely different crystal patterns. The simplest scales are elliptical discs, with sharply etched radiating lines on the proximal surface, and a less clearly defined series of concentric rings or a vague spider's web pattern on the distal side (Pl. 154, figs. 1, 2). Scales of this kind are also well-known in *Crystallolithus hyalinus*, where they provide the support upon which calcite crystals are secreted (Parke and Adams 1960). In addition to these simple scales, most species of *Chrysochromulina* also carry larger and more elaborate scales, in which the distal layer is modified in various ways, often producing a central spine. The large scales of *C. chiton* (Parke *et al.* 1958, figs. 16, 17, 28, 29) are shaped like pie-dishes, with sloping walls on the distal surface, much like those of *Pontosphaera* (Pl. 146, fig. 5). *C. ericina* (Parke *et al.* 1956, figs. 17–19) has scales shaped like rhabdoliths with very long spines, reminiscent of some Tertiary species of *Rhabdosphaera*. In several other species the spines are differently constructed, and do not resemble those of *Rhabdosphaera*, but are

EXPLANATION OF PLATE 153

Figs. 1–8. *Discoaster* spp. 1, *D.* sp. showing crystal faces; each of the six rays is a separate rhombohedron, with triad axis at right-angles to page; No. 22291, Upper Oligocene, core DWBG 10, Pacific Ocean; $\times 6100$. 2, *D. elegans* Bramlette and Sullivan, No. 11890, Middle Oligocene (reworked from Eocene?), Grundf r, Denmark; $\times 3000$. 3, *D. barbadiensis* Tan Sin Hok, No. 11949, Middle Oligocene (reworked from Eocene?), Grundf r, Denmark; $\times 4500$. 4, *D. lodoensis* Bramlette and Riedel, No. 15771, Eocene, Tuilerie de Donzacq, Landes, France; $\times 1900$. 5, *D. strictus* Stradner, No. 11899, Middle Oligocene (reworked from Eocene?), Grundf r, Denmark; $\times 3000$. 6, *D. deflandrei* Bramlette and Riedel, No. 15830, Eocene, Tuilerie de Donzacq, Landes, France; $\times 4000$. 7, *D. hamatus* Martini and Bramlette, No. 16969, damaged specimen, Pliocene, core DWBP 119, Pacific Ocean; $\times 4000$. 8, *D. browneri* Tan Sin Hok, No. 22197, Pliocene, core LSDH 78P, Pacific Ocean; $\times 3000$.

Fig. 9. *Marthasterites tribrachiatus* (Bramlette and Riedel) Deflandre, No. 10485, Lower Eocene, R snaes, Denmark; $\times 2500$.

EXPLANATION OF PLATE 154

Figs. 1–3. *Crystallolithus hyalinus* Gaarder and Markali (= motile phase of *Coccolithus pelagicus*), strain No. LB 913/12 (Plymouth 182), Culture Collection of Algae and Protozoa, Botany School, Cambridge; $\times 16\,000$. 1, No. 22909, two scales in proximal view. 2, No. 22911, two scales in distal view. 3, No. 22915, scale and calcite rhombohedra detached during preparation.

Fig. 4. *Scyphosphaera* sp., No. 18028, ordinary coccolith, proximal view; recent Globigerina Ooze, *Discovery II* Sta. 4269, Biscay Mts.; $\times 6000$.

Figs. 5–7. *Scyphosphaera* sp., ordinary coccoliths; modern Globigerina Ooze, *Challenger* Sta. 338, S. Atlantic Ocean. 5, No. 11316, distal view, $\times 6000$. 6, No. 11317, detail, distal surface. $\times 20\,000$. 7, No. 11308, detail, proximal surface, $\times 80\,000$.



1



2



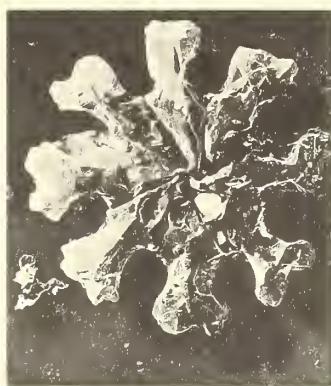
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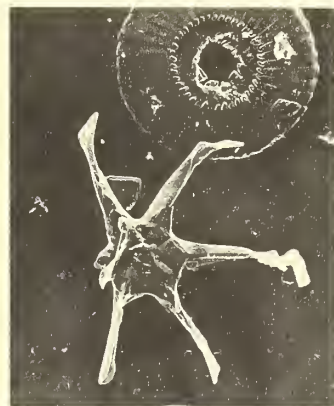
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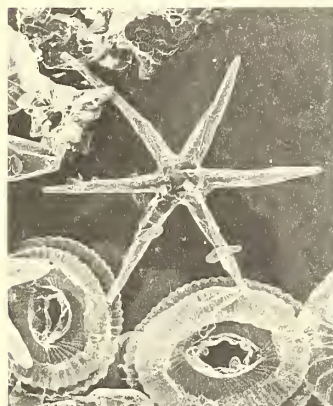
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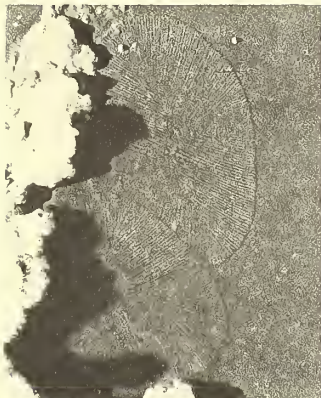
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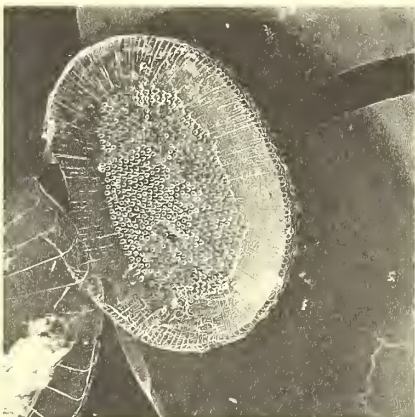
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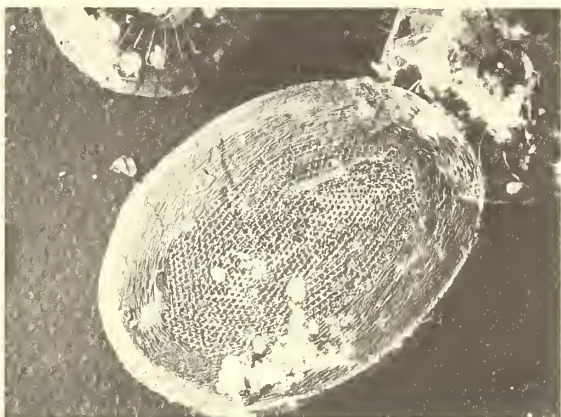
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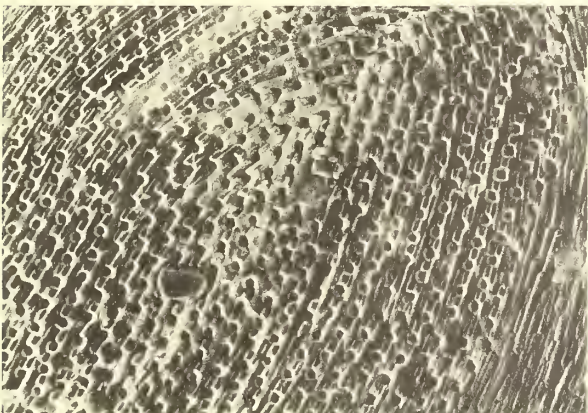
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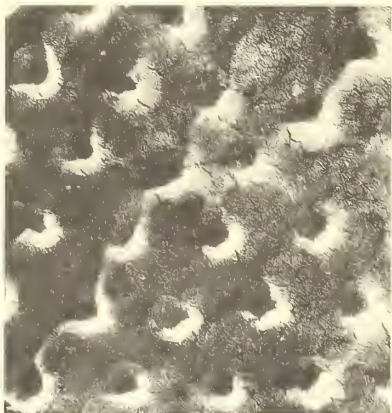
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6



7

remarkably like those of certain Mesozoic genera. In these species the spine is supported by four buttresses which arise from the distal surface of the scale. *C. alifera* (Parke *et al.* 1956, fig. 76) has buttresses which do not reach the marginal rim, much as in the Cretaceous *Eiffellithus* (Pl. 149, fig. 6). In *C. ephippium* (Parke *et al.* 1956, figs. 38, 39) the buttresses are arranged exactly as in the Jurassic *Polypodorhabdus* (Pl. 150, fig. 2); they extend from the marginal rim to the centre, dividing the scale into four quadrants, each of which is ornamented by radial striae on the proximal surface. In the large spined scales of *C. pringsheimii* (Parke *et al.* 1962, figs. 21, 22, 29) the supports of the tall spine are no longer in contact with the surface of the scale except at the outer margin, but behave like flying buttresses; the whole arrangement is an astonishing duplication of the Upper Cretaceous *Deflandrius* (Pl. 151, fig. 3). *C. pringsheimii* is unusual in having so many as four different kinds of scale, each of which could serve as a template for the orderly disposition of calcite-crystals to give a familiar coccolith pattern.

Enough has been said to show that there is a very significant parallel between the calcified and uncalcified Haptophyceae. Several of the living species of *Chrysochromulina* could indeed be regarded as uncalcified survivors of familiar Mesozoic families. It would be asking too much of coincidence to believe that the few living species of *Chrysochromulina* have contrived to reconstruct in their uncalcified scales just those features that were required to start off the Podorhabdaceae in the Oxfordian, the Deflandriaceae in the Albian, and the Pontosphaeraceae and Helicosphaeraceae sometime near the beginning of the Tertiary. I think it is at least as reasonable to suppose that this remarkable genus is indeed a survival from a protean stock that existed in early Mesozoic times, and by selective calcification of its organic scales has given birth to these ancient families.

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APPENDIX

Localities of deep-sea samples mentioned in the explanation of plates

H.M.S. *Challenger*

Station 338: dredge, 21° 15' S., 14° 02' W., about 900 miles S. of Ascension Is., South Atlantic Ocean.

R.R.S. *Discovery II*

Station 3809: dredge, northern slope of Galicia Bank, 42° 56' N., 11° 47' W., about 120 miles W. of Cape Finisterre.

Station 4269: trigger-weight core, Biscay Mts., W. of Bay of Biscay.

Station 4288: dredge, Biscay Abyssal Plain, Bay of Biscay.

Scripps Institution of Oceanography

DWBG 10: core sample, specimens from 11 to 27 cm. 6° 54' N., 131° 00' W., central Pacific Ocean.

DWBG 23B: core sample, specimens from 10 to 12 cm. 16° 42' S., 145° 48' W., between Tuamotu Archipelago and Tahiti.

DWBP 119: core sample, specimens from 398 to 400 cm. $27^{\circ} 54' \text{ S.}$, $106^{\circ} 53' \text{ W.}$, about 200 miles ESE. of Easter Is.

LSDH 78PG core sample, specimens from 250 to 270 cm. $4^{\circ} 30' \text{ S.}$, $168^{\circ} 03' \text{ E.}$, between Gilbert Is. and Solomon Is.

MAURICE BLACK
Department of Geology
Sedgwick Museum
Cambridge

Typescript received 21 May 1968

THE PALAEOONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1967-8

MEMBERSHIP. On 31 December 1967 there were 1,353 members (725 Ordinary, 131 Student, and 497 Institutional), a net increase of 15 members during the year.

FINANCE. During 1967 expenditure rose by £2,724 due largely to the cost of reprinting Volume 3, Part 2 and producing Special Papers. This increase was more than offset by an increase in sales from £1,381 to £4,348. There was also an increased income from subscriptions, interest, and donations to specific papers, but general donations at £525 reached their lowest level.

Special Paper No. 1 was published at a cost of £3,227; donations of £1,500 from the N.C.B. and £250 from Shell Oil Company together with sales of £912 left £565 as a charge on the Publications Reserve at the end of the year. Standing orders for Special Papers now number 135.

Volume 3, Parts 1, 3, and 4 will have to be reprinted as soon as possible and £1,500 has been set aside for this purpose from the Publications Reserve. This now stands at £5,720, enough to cover 62 per cent of a single volume compared with 63 per cent at the end of 1966.

Subscriptions for Ordinary and Student Members were raised to meet the increasing cost of printing *Palaontology* which will rise to over £9,000 in 1968.

PUBLICATIONS. The four parts of Volume 10 of *Palaontology* were published during 1967; they contained 37 papers plus 'Notes for Authors'.

Special Papers in Palaontology No. 1 for 1967 was published; it contained 324 pages and 27 plates.

MEETINGS. Four meetings took place during 1967-8. The Association is grateful to the Council of the Geological Society of London, Professor J. Sutton (Imperial College, London), and Professor Scott Simpson (University of Exeter) for generously granting facilities for meetings, and to Mr. G. W. Green and Mr. M. Mitchell for leading the field meeting.

- a. The *Tenth Annual General Meeting* was held in the Rooms of the Geological Society of London, Burlington House, London, W. 1, on Wednesday, 1 March 1967, at 5.00 p.m. The Annual Report of the Council for 1966-7 was adopted and the Council for 1967-8 was elected. Professor Alwyn Williams of the Queen's University, Belfast, delivered the *Tenth Annual Address* on 'Evolution of the shell structure of articulate brachiopods'.
- b. A *Field Demonstration Meeting* was held at Burrington Combe in the Mendips on Saturday, 6 May 1967. Mr. G. W. Green and Mr. M. Mitchell demonstrated the Carboniferous Limestone succession.
- c. The *Tenth Anniversary Meeting and Dinner* was held at Imperial College, London, on Wednesday, 8 November 1967. The discussion meeting was on 'The explosive development of palaeontology' and the introductory speakers were Professor P. C. Sylvester-Bradley, Dr. D. N. Wood, and Dr. W. S. McKerrow.
- d. A *Symposium* on 'Devonian floras and faunas' was held in the Department of Geology, University of Exeter, on Thursday to Saturday, 14-16 December 1967. About 45 persons attended to hear 16 papers and see 13 demonstrations. Professor Scott Simpson was local secretary.

SPECIAL GENERAL MEETING. Immediately before the Discussion Meeting at Imperial College, London, on Wednesday, 8 November 1967, a Special General Meeting was held at 3.00 p.m. to consider a change in Rule 2 of the Constitution. The following motion was proposed from the Chair and passed (*nem. con.*):

That, effective from 1 January 1968, Rule 2 of the Constitution be amended to read as follows:
'There shall be Ordinary members, Institutional members, and Student members, and their annual subscriptions shall be Five Pounds, Seven Pounds, and Three Pounds respectively. Each subscriber shall be considered a member of the Association, but Institutional members shall not be eligible to take part in the government of the Association.'

COUNCIL. The following were elected members of the Council of the Association for 1967-8 at the Annual General Meeting on 1 March 1967: *President*: Professor T. S. Westoll, F.R.S.; *Vice-Presidents*: Dr. W. S. McKerrow, Professor F. H. T. Rhodes, Professor C. H. Holland; *Treasurer*: Dr. C. Downie; *Secretary*: Dr. J. M. Hancock; *Editors*: Mr. N. F. Hughes, Dr. Gwyn Thomas, Dr. I. Strachan, Professor M. R. House, Dr. R. Goldring; *Other members*: Mr. M. A. Calver, Dr. C. B. Cox, Mr. D. Curry, Dr. Grace Dunlop, Mr. G. F. Elliott, Dr. T. D. Ford, Dr. A. Hallam, Dr. R. P. S. Jefferies, Dr. G. A. L. Johnson, Dr. W. D. I. Rolfe, Dr. A. H. Smout, Dr. L. B. H. Tarlo, Professor H. B. Whittington.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING
31 DECEMBER 1967

BALANCE SHEET

<i>Liabilities</i>	£	s.	d.	£	s.	d.
Publications Reserve Account						
Balance as per Account				5,720	1	8
Special Papers Fund Account				—	—	—
Provision for Reprinting				1,500	0	0
Amounts received in advance of Subscriptions for 1968				451	10	8
Provision for cost of publication of <i>Palaeontology</i> , Vol. 10, as per						
Income and Expenditure Account	7,960	8	10			
Less Expenditure incurred to 31 December 1967	4,860	8	10			
				3,100	0	0
Sundry Creditors				25	5	1
<i>Note.</i> No amount has been included in these accounts for subscriptions unpaid at 31 December 1967						
				£10,796	17	5
<i>Assets</i>	£	s.	d.	£	s.	d.
Office Equipment at cost	27	6	6			
Less Depreciation to date	15	6	6			
				12	0	0
Investments at cost:						
Equities Investment Fund for Charities—958 units	999	18	3			
5 per cent Defence Bonds	2,000	0	0			
Liverpool 6½ per cent Bonds	1,500	0	0			
Wagon Investment Loan 6¾ per cent	2,000	0	0			
5½ per cent National Development Bonds	2,000	0	0			
				8,499	18	3
Sundry Debtors and Payments in Advance:						
Authors for offprints				547	2	11
Advance Payments:						
For <i>Palaeontology</i> , Vol. 11	83	6	8			
For <i>Palaeontology</i> , offprints	84	16	6			
				168	3	2
Cash at Bank:						
Deposit Account	106	17	6			
Current Account	1,462	15	7			
				1,569	13	1
				£10,796	17	5

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above Balance Sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1967 and of its income and expenditure for the year ended on that date.

JOSHUA WORTLEY & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED
31 DECEMBER 1967

<i>Expenditure</i>	£	s.	d.	£	s.	d.
<i>To Provision for the cost of Publication of Palaeontology, Vol. 10</i>						
Part 1	1,925	10	3			
Part 2	2,034	18	7			
Part 3	2,000	0	0			
Part 4	2,000	0	0			
	7,960	8	10			
<i>Add extra costs Vol. 9, Part 4</i>	146	3	4			
	8,106	12	2			
<i>Less over-provision for Vol. 9, Part 3</i>	118	16	9	7,987	15	5
<i>Reprinting Vol. 3, Part 2</i>				554	8	6
<i>Administrative Expenses:</i>						
Insurance	2	0	3			
Postages and Stationery	191	13	6			
Audit Fee	14	14	0			
Honorarium to Assistant Treasurer	120	0	0			
Duplicating and dispatch of circulars	181	10	2			
Meeting expenses	32	9	3	542	7	2
<i>Depreciation of Equipment</i>				6	0	0
<i>Special Papers:</i>						
Printing costs	3,319	7	9			
<i>Less Sales</i>	920	9	11			
<i>Donations:</i>						
Shell	250	0	0			
Foreman	475	8	9	1,645	18	8
<i>Excess of Income over Expenditure transferred to Publications Reserve Account</i>				1,578	13	9
				<u>£12,342</u>	<u>13</u>	<u>11</u>

<i>Income</i>	£	s.	d.	£	s.	d.
<i>By Subscriptions for 1967</i>	5,923	11	8			
Subscriptions for 1966	<u>202</u>	<u>0</u>	<u>3</u>	6,125	11	11
Sales of Publications				3,428	15	2
Interest received:						
5 per cent Defence Bonds	260	0	0			
Bank Deposit Account	30	18	2			
Equities Investment Fund for Charities	76	4	10			
Liverpool Corporation	101	9	0			
Wagon Investments	<u>124</u>	<u>18</u>	<u>4</u>	593	10	4
Special Donations				217	14	7
General Donations:						
British Petroleum Co.	250	0	0			
Texaco	175	0	0			
Burmah Oil Co., Ltd.	<u>100</u>	<u>0</u>	<u>0</u>	525	0	0
Miscellaneous Receipts				66	11	11
Special Papers Fund				1,385	10	0
Excess of Expenditure over Income transferred to Publications Reserve Account						
				<u>£12,342</u>	<u>13</u>	<u>11</u>

PUBLICATIONS RESERVE ACCOUNT

<i>To Balance as per Balance Sheet</i>				5,720	1	8
Excess of Expenditure over Income				—	—	—
Provision for Reprinting				—	—	—
				<u>£5,720</u>	<u>1</u>	<u>8</u>
<i>By Balance at 31 December 1966</i>				5,141	7	11
Add Excess of Income over Expenditure	1,578	13	9			
Less Provision for Reprinting	<u>1,000</u>	<u>0</u>	<u>0</u>	578	13	9
				<u>£5,720</u>	<u>1</u>	<u>8</u>



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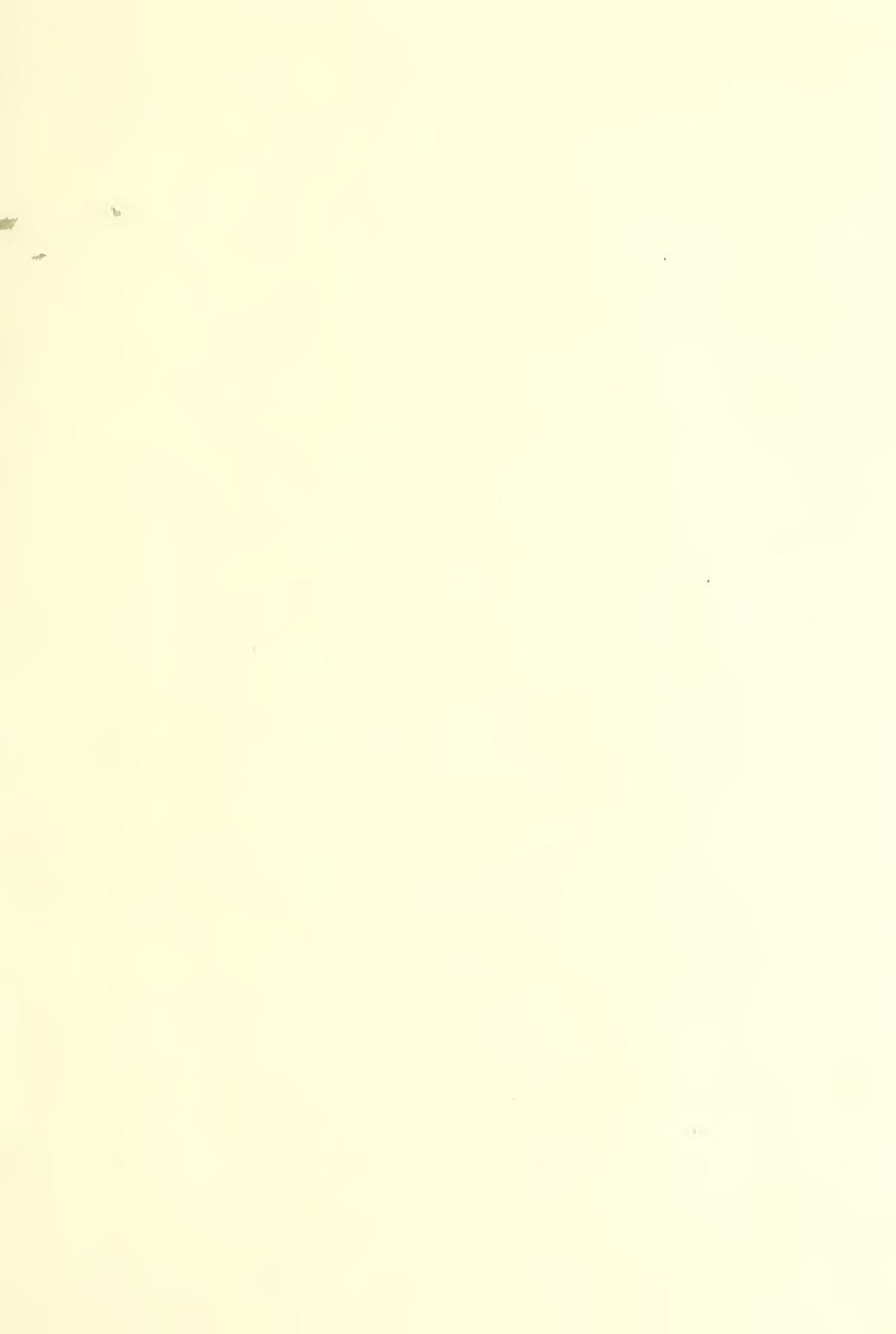
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